

The Journal of Comparative Neurology and Psychology

(Continuing the Journal of Comparative Neurology)

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C. L. Harwick

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Volume XIV.

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Number 1.

THE RELATION OF THE MOTOR ENDINGS ON THE MUSCLE OF THE FROG TO NEIGH- BORING STRUCTURES.

By JOHN GORDON WILSON, M.A., M.B., (Edin.)

(From the Hull Anatomical Laboratory of the University of Chicago.)

With Plates I and II.

It is obviously a matter of some importance in the study of the relation of nerve excitability to muscle contraction, to determine the manner in which the peripheral part of the neurone is related to the muscle fiber. Nor has it been neglected; it has long been a favorite subject for investigation and a prolific field for speculation and debate. At the present time renewed attention is being called to it by the recent works of APÁTHY, RUFFINI, GRABOWER and others. In these writings special emphasis is being laid on the presence of fine fibrillae, called by RUFFINI ultra-terminal fibrillae, which are projected from nerve endings to various neighboring parts.

From an historical standpoint it is extremely interesting to compare the results of KÜHNE with those of RUFFINI, DOGIEL, HUBER, SIHLER and others, and to observe that as methods and technique improve, a corresponding complexity can be shown in the relation of nerve to muscle. This is well exemplified in the ending of the motor neurone on the frog's muscle. As regards this animal one must acknowledge that the remarks of APÁTHY on nerve endings in invertebrate muscles are not inappropriate:—

“Wenn ich auch hier und da schlechthin von Nervenendigungen spreche, so will ich doch gleich hier von vorn herein betonon, dass ich eine Endigung der leitenden Primitivfibrillen nirgends mit Sicherheit constatiren konnte; ich kann nur sagen, bis wie weit ich eine leitende

Primitivfibrille, oft wohl bereits Elementarfibrille, an einer bestimmten Stelle meiner Präparate zu verfolgen im Stande bin." ¹

In 1877 GERLACH described the nerve endings of the frog as branching dichotomously to form an intravaginal network which runs through the contractile substance of the muscle fiber in close relation to, if not in actual continuity with, the contractile fibrillae. He appears to have been influenced in his deductions by the fact that in staining with gold chloride, he obtained reactions from certain elements of the sarcous substance which were similar to those obtained in nerve endings. In 1889 he repeated these investigations with methylene blue, and claimed that this method substantiated his previous views. Subsequent research by others has not confirmed his results nor upheld his deductions; nor can his own drawings be said to support the claims he attempted to establish. To one conversant with *intra-vitam* staining with methylene blue, it will appear a very doubtful procedure to base results on the similarity of staining reactions. By this *intra-vitam* method one constantly sees fine blue-stained fibers in the intermuscular connective tissue which, taken alone, might simulate nerve fibrillae. At times one observes beautifully stained examples of myofibrillae either as very fine closely-arranged points or as continuous structures. On this ground alone, therefore, it is obvious that it would not be possible to deduce a nervous plexus either within or without the muscle-cell. In addition, there must be present an undoubted continuity of structure with an unmistakable nerve fiber, together with any characteristic appearance which one is accustomed to find in corresponding terminals.

In 1896 APÁTHY drew attention to the manner in which the axis cylinder divides in invertebrate muscle fibers. He describes the primitive fiber as entering the muscle cell and there dividing into fine fibrillae (primary fibrils). These, however, do not form a plexus but either send comparatively thick branches (secondary fibrils) to adjacent muscle-cells there to form terminations from which it may be that further branches

¹ *Mittheil. a. d. Zoolog. Station zu Neapel.*, Bd. XII, 1896, p. 505.

(tertiary fibrils) may proceed to other muscle cells; or they divide repeatedly into ever finer fibrils till ultimately perhaps, elementary fibrillae result. He often saw very fine nerve fibrillae pass out of a muscle cell into the neighboring connective tissue and it might be, branch there. As to the ultimate fate of the finest fibrillae he is uncertain, but he declares: "Es kommt mir an wahrscheinlichsten vor, das sie mit anderen ähnlichen ein intermuskuläres Elementargitter bilden." ¹

The results of APÁTHY led RUFFINI in 1900 to re-examine nerve endings in the human muscle which he had stained by his chloride of gold method. Here he found in some of his specimens fine fibers which he had not previously noted and which he now described under the name of ultra-terminal fibrillae. These are very fine, non-medullated fibrillae which pass out from the motor end-plate. "This fibrilla" (ultra-terminal), he says, "after an unbranched course, more or less long, may terminate in the same muscular fiber on which rests the plate from which it is derived, or, as is often the case, put itself into relation with one of the neighboring striated fibers. From it collaterals may at times come off." It may end in a swelling or in a second small plate (plaquette); in one case from a plaquette another fibre was seen to pass out, but its course could not be followed. Summing up the results of his examination, he says: "The motor plates in man do not represent the true and real terminations of motor nerves, because beyond the plate there exists a well demonstrable anatomical continuity shown by non-myelinated nerve fibrillae of which we do not know the last relations." ² This is obviously a statement very closely akin to that given by APÁTHY in the summing up of his results.

Later PERONCITO, working with RUFFINI and using his gold chloride method, describes in *Lacerta muralis* and *Lacerta viridis* the ultraterminal fibrilla as separating itself from the

¹ *Ibid.*, p. 695.

² RUFFINI: Sulle fibrille nervose ultraterminale nelle piastre motrici dell'uomo. *Rivista di pat. nerv. e ment.*, 1900, V. 5.

nerve fiber at the point where it loses its medullary sheath and penetrates the motor plate; from here it may pass to end on a muscle fiber or in a neuromuscular spindle.

In any discussion on nerve endings it is well to recognize the facts that are universally accepted. Thus it is well established that a motor nerve may branch repeatedly before ending, or to put it otherwise, the peripheral ending of a motor neurone is connected with many muscle fibers. This branching occurs at a node. Each branch is a medullated fiber smaller in calibre than the parent stem and it ultimately loses the medullary sheath and breaks up to form a nerve ending usually on one muscle fiber, to which it alone is attached. To this very general statement there are a variety of exceptions. Thus, two or more endings may go to one muscle fiber; or a non-medullated nerve may pass off from a node; occasionally, though more rarely, a non-medullated nerve may be seen leaving a medullated nerve where no node is apparent. To define concisely and yet accurately the term motor nerve ending, either from an anatomical or physiological standpoint, is in the present state of our knowledge by no means easy. For our present purpose a motor ending may be regarded as that peripheral part of the nerve which, on reaching a muscle fiber, loses its medullary sheath and breaks up into more or less numerous non-medullated¹ branches or end-twigs which enter into a more or less close relation to the muscle fiber. Having thus defined a motor ending, the significance of the term ultraterminal fibrilla is the better understood; this is a fine non-medullated fibril which passes from one of the twigs of the nerve termination to a region beyond the primary ending. Here it enters into relation with the muscle fiber on which rests the ending from which it originally sprang, or with some adjacent muscle fiber or with a neighboring muscle spindle.

¹ DOGIEL has described a medullary sheath as occurring in the nerve ending (*Archiv f. mikr. Anat., Bonn*, 1890, p. 314). This I have never seen, though the dye oozing from the axis cylinder at times gives a resemblance to such.

The following investigations were undertaken by me to determine how the motor nerve endings on the muscles of the frog are related to other structures; and also to ascertain, as far as possible, how the terminal nerve fibrils finally break up and disappear. Especially did it appear necessary to compare the results observed by RUFFINI and others using gold chloride methods with the results obtained by the *intra-vitam* methylene blue method.

Method: The muscles of the frog used were either the M. sartorius, the M. peroneus or the M. tibialis anticus. Into these was injected with a hypodermic syringe, a very weak solution of methylene blue in various salt solutions, for this research has been carried on as a preliminary part of an investigation on the effect of various salts and poisons on motor nerve endings. Grammolecular solutions of the following salts, among others, were used: sodium chloride, sodium carbonate, sodium ammonium phosphate, magnesium sulphate. Nerve endings can be obtained by a solution of methylene blue in distilled water, or with methylene blue in solution with any of the above salts; but the most constant and best results are obtained if sodium chloride is present in the solution. So far as the present paper is concerned, the following solution was constantly employed:

Methylene blue (GRÜBLER's nach EHRLICH) 0.5% sol.	1 or 2 cc.
Sodium chloride solution, 0.58% sol.	2 cc.
Aqua destil.	17 cc.

This was found to be the most suitable strength of methylene blue to use, though one of half this strength often answers well, especially for sensory endings and sympathetic plexures on blood vessels. The largest and most complex endings were seen when the muscle was injected with the above solution after there had been added to it a few drops of a weak alkaline salt, such as sodium ammonium phosphate, and then a very weak faradic current passed through the nerve trunk for a few seconds.

A few minutes after injecting the solution the muscle is cut out and exposed on a glass slide which has been moistened

with normal salt solution. Within a varying time, usually about five minutes, the nerve endings begin to appear. As soon as these are well marked the muscle is fastened to cork and placed in ammonium molybdate solution (5%) at a temperature near freezing point. Temperature plays a very important part in the subsequent treatment of the tissues. If it rise at any point of the procedure—e. g. when washing in water or passing through alcohol—the methylene blue dissolves out from the very fine fibrillae. If the tissue has to be kept over night in molybdate it is well to place it, especially in summer, in a refrigerator. When passing through alcohol, the vessel should be surrounded by ice-cold water.

The addition of HCl to the molybdate solution is not necessary; I have found it even a disadvantage for the finer results. BETHE in his recent work has abandoned its use.

After removal from the molybdate, the muscle, if too thick, is cut in a freezing microtome, examined in water, and only that part kept which shows traces of nerve endings. The tissue is now passed through 95% and absolute alcohol, preferably, as stated above, at a low temperature; then from xylol into paraffin. It is important that it remain sufficiently long in xylol to remove the alcohol; otherwise the temperature of the melted paraffin will cause any alcohol present to remove the methylene blue from the fine fibrillae. It remains in paraffin for two hours. The thickness of the section varies with the object aimed at. To get long stretches of nerve endings, it is best to cut from 20 to 50 micra; if one wish to study the relation of the endings to the muscle cell, a thickness of from 5 to 10 micra must be used.

After numerous experiments with various dyes as a counterstain, the following was found most suitable, inasmuch as it dyed the muscle fiber an orange, the sheath of HENLE a rose-pink and the neurilemma a faint pink:

Acid fuchsin	1 g.
Orange "G"	6 g.
Alcohol, absolute,	60 cc.
Aqua destil.	240 cc.

In the frog's muscle the nerve ending has no ground plate in which the branches ramify. The ramifications are not localized but are spread over a relatively large and apparently variable area of the muscle fiber. Usually but one medullated nerve ends in a muscle fiber, though two medullated nerves may be seen at times and three have been described; occasionally two medullated nerve fibers and one non-medullated and much finer fiber may go to the muscle fiber. When more than one nerve goes to a muscle fiber it is often possible to trace the origin of these to the same nerve stem. In no case was there even the suggestion of one of these fibers coming from a nerve whose course lay distinctly apart from the others. If more than one nerve go to the muscle fiber, the places where the nerves enter into contact with the fiber are, if not always, at least most frequently, in close proximity to one another. In short, on the muscle fiber the area to which the entering nerves apply themselves relative to the entire length of the muscle fiber is limited.

Several varieties of motor endings have been described. Thus, there are the four or five types of CUCCATI which RETZIUS would reduce to two; the one exemplified by the branching plate, the other by the broad band. At present, any classification must be but temporary; with equal justification several varieties may be classed as typical by one and rejected by another. For example, one might well wish to add to the types of RETZIUS that more strictly localized variety which DOGIEL has described and which occurs not unfrequently in certain muscles—a variety which closely resembles the branching of mammalian nerve endings only without an end plate.¹

There is, however, one type which is generally recognized as predominating—*das Stangen-geweih* of KÜHNE. In it the nerve after losing its medullary sheath divides more or less dichotomously and spreads itself along the length of the muscle fiber. The band variety is less common; one notes that the better stained the preparation the less frequently it appears.

¹ *Arch. f. mikrosk. Anat.*, 1890, Bd. xxxv.

In the frog the end-arborizations do not terminate necessarily on one muscle fiber. It is not unusual to find that, while the majority of the terminal fibers confine themselves to one muscle fiber and to a certain definite area, one or more fine non-medullated fibrillae pass far beyond the area or to a neighboring muscle fiber. So common is this that in well stained preparations one is ever expectant of finding at least traces of such fibrillae. They are often difficult to observe; but the cause of this is not so much that they do not readily stain, as that it is hard to fix the dye and easy to have it extracted during the stages subsequent to fixation.

Such non-medullated fibrillae may be termed ultraterminal. A convenient way to describe them is to classify them according to the manner in which they end, so far, at least, as such can be traced at present. With this in view, we might describe them as follows:

- (1) Relatively thick, non-medullated fibers which pass to adjacent muscle fibers and divide into endings which resemble more or less closely, though much smaller, the dichotomously branching arborizations from which they spring. These come off very soon after the primary axial fiber loses its medullary sheath and begins to break up (Fig. 1; Fig. 4; Fig. 6).
- (2) Fine fibrillae which pass from the nerve ending into the inter-muscular connective tissue and there cease to be capable of being followed farther (Fig. 1; Fig. 3; Fig. 2).
- (3) Very fine non-medullated fibrillae which detach themselves at various points of the terminations and pass to end in adjacent muscle-fibers in one of the following ways:
 - a) by getting so faint and so fine that it becomes impossible to follow them farther (Fig. 1; Fig. 2; Fig. 3).
 - b) by terminating at what appears as a much thickened knob (similar to Fig. 1, B and C)
 - c) by breaking up into a plexus from which some at least of the fibrillae disappear in the muscle fiber while others continue on (Fig. 2)
 - d) by forming a plexus which enters into close relationship with a typical nerve ending (Fig. 3)
 - e) by breaking up after a relatively long course to form a small localized ending, each termination of which is furnished with a knob (Fig. 6).

At no time have I seen any appearance of an intermuscular nerve plexus formed by these fibrillae. I am inclined to regard the motor fibrillae which pass into the intermuscular connective tissue and there disappear, as either broken fibrillae or fibrillae only partially stained.

The relation of the nerve ending to the muscle fiber.—The relation of the nerve endings to the sarcolemma has been much disputed. Of recent writers who have discussed this question with reference to the muscle of the frog, the following only need to be referred to: HUBER-DEWITT,¹ after a careful investigation, come to the conclusion that the terminals lie under the sarcolemma and are devoid of any sheath. SIHLER,² on the other hand, using a method which he finds particularly applicable to this research, considers that the endings lie over the sarcolemma and that the end of fibrils are covered "down to their tips with the sheath of SCHWANN;" further that the sheath of HENLE is open (*verwächst mit nichts*) and does not cover the end fibrils, but that the nerves emerge from it as an arm from a sleeve (*wie der Arm aus dem Aermel*); at the same time, he does not deny that there are points where the nerve substance and the muscle fiber may come into contact.

In fresh muscle fibers in which the nerves have been stained by the *intra-vitam* methylene blue method, I have found that, while the majority of the terminal branches lie in close relation to the muscle fiber, at times a terminal fibril is seen to rise some distance above the muscle fiber, and occasionally such a nerve fibril sends down to the muscle fiber little rootlets comparable to those described by SIHLER. But sooner or later even in such nerve fibrils the ultimate terminals come to lie on the muscle fiber. While the occurrence of such nerve fibrils may be held to prove that the larger fibrils may be epilemmal, there is nothing to show what the relation of the terminal fibrils

¹ HUBER-DEWITT: Nerve Endings in Muscles. *J. Comp. Neurol.*, 1897, VII, p. 185.

² SIHLER: (a) The Nerves of the Capillaries with remark on Nerve Endings in Muscles. *J. Exp. Med.*, 1901, V, p. 511. (b) Neue Untersuchungen über die Nerven, etc. *Zeit. f. wiss. Zool.*, Leip., 1900, LXVIII, pp. 351 and 375.

to the muscle fiber may be. To investigate this a much higher magnification and a more differential stain are necessary than at present are available in the examination of fresh tissues.

By means of the orange G acid fuchsin counterstain above referred to, I have found it possible to distinguish clearly between the nerve fiber (blue), the sheath of HENLE (rose-pink), the faintly stained neurilemma (pink), and the muscle fiber (orange). In thin sections (5 to 7 μ) examined by the 1-12 ZEISS oil immersion lens, where the medullated nerve was observed to lose its medullary sheath and divide into the primary branches, I often clearly saw the primary branches, especially when they were lying in the upper edge of the muscle fiber, enclosed by the neurilemma and by the sheath of HENLE. Moreover these sheaths could at times be traced for some distance on the primary divisions of the ending. The differentiation of the two nerve sheaths was at times aided by the fact that one could distinguish the attachment of the neurilemma to the node, as described by BOVERI and BETHE,¹ while the sheath of HENLE had no such attachment but was continuous over the node. This condition was seen in the section from which Fig. 7 was obtained. Here the neurilemma attached itself to the node where the medullary sheath ceased, and thence was continued over the fibrils. For this research it was not necessary to determine whether at the node the neurilemma was or was not interrupted. Outside of this lay the sheath of HENLE. Each sheath could be followed separately to the muscle fiber, where together they applied themselves to the sarcolemma. When so applied to the muscle fiber, it was not possible to distinguish with accuracy between the pale stained neurilemma and the strongly stained sheath of HENLE. But it was possible to see clearly that the sheath round the nerve was distinct from and was placed outside of the sarcolemma—a distinction which was aided by the fact that here the sheath of HENLE stained at times more strongly than it had previously done and appeared as if it were there thickened

¹ BETHE: *Anatomie und Physiologie des Nervensystems*, 1903, p. 50.

or compressed. As the fibrils subdivided each branch was surrounded by a sheath which became fainter as the nerve fibril became finer.

Occasionally there coiled round a primary terminal branch of a nerve ending another nerve in no way related either to this nerve ending or to its muscle fiber. Thus in Fig. 5 at (2) the nerve (3) curved round a primary terminal division of the nerve termination on muscle fiber A. This is only to be explained by one of two suppositions; either both nerves at that point were over the sarcolemma or under it. The latter supposition is open to many objections; the former will generally be acknowledged to be the more probable, and to me is a confirmation of what I have already stated.

Attention was now directed to two points:

- (1) The relation of terminal fibrillae and of the end knobs to the sarcolemma;
- (2) The relation of the ultraterminal fibrillae to a sheath.

In sections where very fine fibrils were seen, one could trace the blending of the nerve sheath with the sarcolemma. In Fig. 9 the terminal nerve fibrilla rested on an apparently homogeneous substance which was not separated from the contractile muscle substance by any sarcolemma and which was covered by a cap formed by the blending of the nerve sheath with the sarcolemma. In short, it lay under the sarcolemma. When the section from which Fig. 9 was drawn, was carefully examined under the 1.5 mm. ZEISS apochromatic and Oc. 6, the sarcolemma appeared at (*a*) to split into very faint lines. Two of these were seen to project as at (*a*) and disappear in the covering cap. Similarly at (*b*) a line was seen to go off as delineated. The impression formed by the study of this and of other similar sections, was that though the cap over the terminal nerve fibrilla or end-knob was formed by the blending of the sheath which surrounded the nerve fibril with the sarcolemma, the tissue which had principally to do with its formation was the sheath of the nerve fibril.

The relation of the root-like knob to the muscle fiber was sometimes particularly interesting. It seems to lie more in the

sarcolemma than under it, though at times a knob could be observed to penetrate deeper towards the fibrillated sarcous substance. It was noted that in every ending the fibrillated sarcous substance was sharply marked off, so that it was always easy to determine that the nerve terminals did not penetrate within or even as far as the fibrillated muscle substance.

On the ultraterminal fibrillae a sheath could at times be seen. This sheath followed closely the convolutions of the nerve, and could be traced to the neighboring muscle to which the nerve was going; there it blended with the sarcolemma. The nerve terminals and end-knobs differed in no respect from the corresponding parts of the main nerve stem (Fig. 6).

In short the primary divisions of the nerve ending lie over the sarcolemma, and are surrounded by both the neurilemma and the sheath of HENLE; the ultimate fibrils lie in a homogeneous substance within the sarcolemma, and are covered by a cap formed by the blending of these sheaths with the sarcolemma. The open condition of the sheath of HENLE, as described by SIHLER, was not observed.

Conclusions.

The so-called nerve ending of the frog is to be regarded in the first place as the peripheral separation of the contents of the axis cylinder, by which separation it is able to spread itself over a relatively wider area. As a nerve fiber may attach itself to various muscle fibers, so the fibrillae of the ending may likewise reach over to adjacent muscle fibers. Those fibrils which detach themselves near the central point of separation are, as a rule, larger and more easily stained than the more distal ones, and are comparable to the non-medullated fibers which may arise from the medullated nerve stem. One can note that the secondary endings to which they give rise are often comparable in form to the primary endings, though having a smaller number of branchings; this would suggest that the amount of branching which is possible bears a relation to the diameter of the fiber.

A plexus is often formed by the nerve terminations (Fig.

5, Fig. 3, Fig. 6.). Whether this is merely an interlacing or a true anastomosis, it would be difficult to decide. The close approximation of some of the terminals and the way in which they run together (Fig. 6) suggest at least a very intimate relationship between them. By means of this plexus arrangement we can well understand how effective the nerve impulse may become. From this network fibrillae may pass to other muscle fibers (Fig. 3, Fig. 6).

Not only in the fixed but in the unfixed preparations the larger branches of the endings are seen to lie over the sarcolemma and even at some distance from it (Fig. 1, Fig. 7). In fresh preparations one occasionally sees a terminal lying over the paler stained yet clearly outlined muscle fiber, and sending down root-like structures to the muscle fiber. The neurone enters into intimate relationship with the muscle fiber either at the peripheral termination of the ending, where each termination appears as a very fine fibrilla to which an end knob or bulb may be attached (Fig. 1, B & C, Fig. 9) or at the terminal knob of each of those root-like structures which at times are projected from the fibrils of a nerve ending. The former termination, including both the terminal fibrilla and its knob, lies in homogeneous substance under the sarcolemma; it is covered by a cap into whose formation there enters both the nerve sheath and the sarcolemma, though chiefly the nerve sheath. The latter termination is in close opposition to the sarcolemma and may be either in or under it.

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EXPLANATION OF THE DRAWINGS.

I am much indebted to Mr. LEONARD H. WILDER for the carefulness and accuracy with which he has prepared the drawings which illustrate this paper.

PLATE I.

Fig. 1. ZEISS D, Comp. occ. 4. The peripheral termination of a neurone, showing Terminal fibrillae with end knobs (1) and (2), Ultraterminal fibrilla ending in intermuscular connective tissue (3), Ultraterminal fibrilla ending on a separate muscle fiber (4).

The medullary sheath, as sometimes happens, is faintly yet distinctly outlined surrounding the continuous and well-marked axis-cylinder. There are three muscle fibers, A, B and C, to which go two medullated nerves, *a* and *b*. The main stem of *a* breaks up on C at 5 into three primary fibrils. In its course there are given off to A two medullated branches, which lose their medullary sheath soon after leaving the main stem and which break up more or less dichotomously. From the one on the left, a non-medullated terminal branch (3) passes beyond the muscle fiber to disappear in the intermuscular connective tissue. The main supply of B is *b*; but the medullated nerve, *a*, while passing over B gives off two very fine, apparently non-medullated branches, one of which ends on B, the other passing to end on C. The termination of the medullary sheath of *a* was close to the breaking up of the axis-cylinder at 5. One of the primary terminal branches on the right gives off a branch 4 which divides dichotomously on muscle fiber B. The others call for no special remark.

Fig. 1, B and C. ZEISS 1-12 oil immersion; Comp. occ. 4. Two forms of endings frequently presented at the terminals of very fine fibrillae.

B. Drawn from (1), shows the fibrillae breaking up into a granular net-like structure.

C. Drawn from (2), shows an elongated broadened club-like body with a marked central axis, imbedded in a well-defined granular mass and surrounded by a homogenous capsule, comparable to cap seen in Fig. 9.

Fig. 2. ZEISS D, Comp. occ. 4. Nerve ending with ultra-terminal fibrillae.

The medullated nerve *a* loses its medullary sheath and breaks up on B at (1). It gives off at (2) a large non-medullated branch which also breaks up on B. The nerve endings send ultraterminal fibrillae to three muscle fibers. The terminal branches to the right could be traced to a distance twice as far as represented. Several of these endings showed knobs similar to those repre-

sented in Fig. 1, B and C. A separate non-medullated nerve (*n*) is shown which forms a small plexus on B, one fiber of which penetrates to a lower plane than the others and ends by forming under the sarcolemma a knob like Fig. 1, B; the other fibers pass on, one to end on B, the other on C.

Fig. 3. ZEISS D, Comp. occ. 4. Three medullated nerves (*a*), (*b*) and (*c*), which pass to three separate muscle fibers, A, B and C, and which have ultraterminal fibrillae and interlacing of endings. Muscle fiber B is seen only in part.

Fig. 4. ZEISS D, Comp. occ. 4. The type of ultraterminal fibrillae seen most frequently.

Fig. 5, A. ZEISS D, Comp. occ. 4. An ending forming a complex network on muscle fiber C. A nerve coiling round the primary terminal divisions of another nerve (compare page 11 on relation of nerve to sarcolemma). The nerve *n* goes to two muscle fibers, A and C. The nerve 3 on which no medullary sheath was seen divides into two branches; one of these ends undivided, the other separates into two branches which run close together and parallel. At (2) the upper branch coils round a primary fibril of the nerve ending on muscle fiber A; in addition it gives off a fibril which disappears in adjoining connective tissues.

Fig. 5, B. Part of Fig. 5, marked (1), drawn with ZEISS oil immersion 1-12 Comp. occ. 4.

PLATE II.

Fig. 6. ZEISS 1-12 oil immersion, Comp. occ. 4. Sections cut 10 μ . Nerve endings shown only in part, with ultraterminal fibrillae (1), (2) and (3), one of these (1) with sheath. The main fiber is seen at *n*. From it a branch to the right passes off and soon divides; one of these divisions has been cut by the sectioning, the other (1) passes to an adjoining muscle fiber, there to end in a small termination like an end-plate with end knobs. The nerve sheath could only be traced distinctly to the point where the nerve enters into contact with the muscle fiber.

Fig. 7. ZEISS 1-12 oil immersion, Comp. occ. 4. Section 5 μ . Stained in orange G, acid fuchsin. Part of nerve ending lying over sarcolemma. This dye colors the sheath of HENLE rose-pink, the neurilemma pink, and the muscle fiber orange. The medullary sheath was apparent at M just above the node R, where the axis-cylinder divides into three branches which pass to the muscle fiber. The sheath of HENLE (H) is seen continued over R without attachment, and two of its nuclei (Hn) were distinctly outlined. Within the sheath of HENLE and closely applied to the axis-cylinder, lay the neurilemma N, attached to the node R. The primary terminal fibrils surrounded by the sheaths lie over the sarcolemma which is distinctly marked beneath the sheath.

Fig. 8. ZEISS apochromatic 1.5, Comp. occ. 6. Section 7.5 μ . A primary terminal fibril with sheaths. H, HENLE's sheath; N, neurilemma; S, sarcolemma.

Fig. 9. ZEISS apochromatic 1.5, Comp. occ. 6. Section 5 μ . A terminal knob lying under the sarcolemma and covered by a cap which is chiefly composed of the nerve sheath. Fine fibers pass at (*a*) and (*b*) from the sarcolemma to blend with the nerve sheath in the cap.

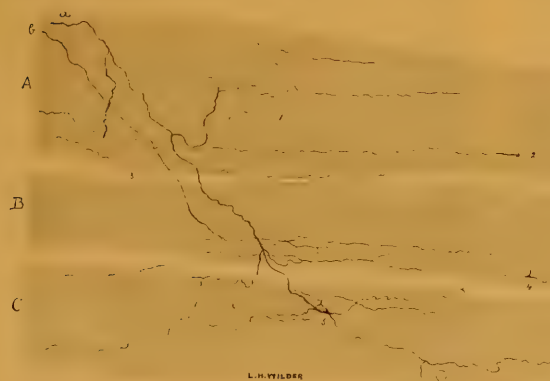


Fig. 1 A



5 B

Fig. 5 A

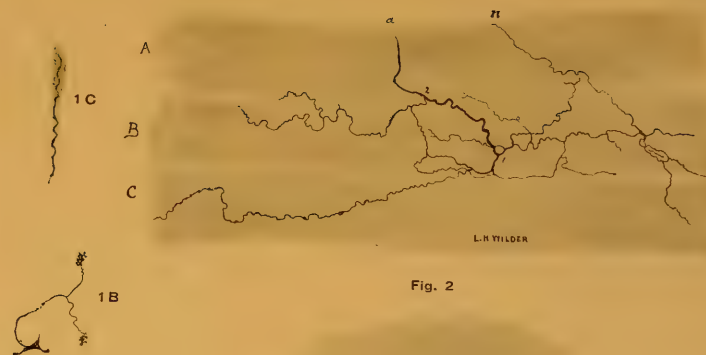


Fig. 2



Fig. 4

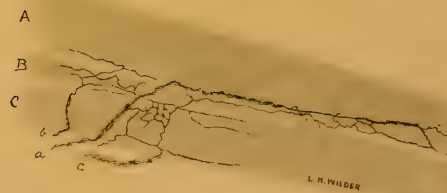


Fig. 3



Fig. 7.

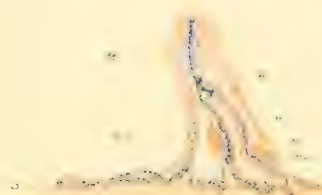


Fig. 8.



Fig. 9.



Fig. 9.

L.H. Wilder, del.

SPACE PERCEPTION OF TORTOISES.

By ROBERT M. YERKES.

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The Sense of Support in Animals.

A number of investigators have noticed that the young of many animals possess a sense of support, and that their behavior is adapted to the spatial conditions in which they happen to be placed. It is this sense of support that saves the sightless kitten or puppy from falls; but in case of the young chick which similarly hesitates when it approaches the edge of a void visual stimuli apparently determine the reaction. These reactions to spatial conditions are controlled by a *complex* of sense impressions which is still unanalyzed. In certain animals visual impressions seem to be all-important; in others organic data are chiefly significant, and again in other organisms there are indications of degrees of sensitiveness, if not modes of sense, of which we have no direct knowledge. And so, strange as it may seem, the "spatial worth" of sense data, as JAMES would call it, is no more a matter of accurate knowledge than is the development of the sense of space, or the modes of behavior in different spatial conditions exhibited by any animal.

THORNDIKE ('99, p. 284), who has studied the behavior of young chicks with reference to spatial relations, says "If one puts a chick on top of a box in sight of (his fellows below, the chick will regulate his conduct by the height of the box." A chick 95 hours old does not hesitate to jump off at heights of 1 to 10 inches; at 22 inches it often hesitates a long time, and at 39 inches it usually does not jump at all. Furthermore, immediately after hatching, young chicks are able to peck at objects with considerable accuracy, and they apparently estimate distances fairly well before they have had much experience outside the shell.

The behavior of young pigeons, chicks, kittens and puppies in unusual spatial conditions has been studied most fully by MILLS ('98, p. 150), who in discussing the 'sense of support' writes: "I have found in the case of all puppies, and several other kinds of animals examined, that even on the first day of birth they will not creep off a surface on which they rest, if elevated some little distance above the ground. When they approach the edge they manifest hesitation, grasp with their claws or otherwise attempt to prevent themselves falling, and, it may be, cry out, giving evidence of some profound disturbance in their nervous system.

"It would seem that there is no more urgent psychic necessity to young mammals than this sense of being supported. All their ancestral experiences have been associated with *terra firma*, so that it is not very surprising that when *terra firma* seems about to be removed they are so much disturbed. To my own mind this is one of the most instructive and striking psychic manifestations of young animals, though I am not aware that any attention has been called to it before; and instead of referring to it under any of the usual divisions of sense, as the muscular sense, pressure sense, etc., I prefer to treat the subject under the above general heading (Sense of Support), for it seems to me that the feeling is a somewhat complex one.

"It is interesting to note that a water tortoise I have had for a number of years will at any time walk off a surface on which he is placed. But this is not a creature that always is on *terra firma* in the same sense as a dog, but it frequently has occasion to drop off logs, etc., into the water. But again, I find this sense of support well marked in birds which drop themselves into 'thin air'. Nevertheless, a consideration of ancestral experiences throws light on most cases, and perhaps on this one also."

Concerning white rats, SMALL ('99, p. 93) states that "as early as the second day (after birth) they show an uneasiness when on the edge of a void—sometimes drawing back, sometimes manifesting their dominant trait of curiosity by leaning over and sniffing. At the age of four or five days the presence

of this sense (the sense of support) is unmistakable, and is not due to experience, as I have found by trying rats that have had no such experience." And WATSON ('03, p. 40) remarks that a rat that wanted to get down from the top of the food box "would usually stretch his head down two or three times, then pull himself back, as though he feared to attempt such a dangerous a feat."

The observations quoted indicate the possibility of interesting studies of the development of space perception in animals, and of such analyses of the sensory complex as shall exhibit the 'spatial worth' of each kind of sense data. Partly for the purpose of making an approach to the comparative study of space perception, partly for the solution of the following specific problems I have observed the behavior of several species of tortoises with respect to spacial conditions. The question which really led to the investigation was, What relation do the reactions of tortoises to space bear to their habits? Does the water species behave in essentially the same manner as does the land-inhabiting form? The attempt to answer this question led to the study of the general behavior of different species, and of the importance of vision and the 'sense of support' in reactions to space.

Relation of Reactions to Space to Habits in Tortoises.

My method of experimentation was to place a tortoise in the middle of a board 30 cm. by 60 cm. which was elevated 30 cm., 90 cm. or 180 cm. above a net of black cloth into which the animal fell when it crawled or plunged over the edge of the board. The fall was thus rendered harmless to the animals, and they gave no evidence, by increased hesitancy in crawling off, that it was disagreeable to them. The observer carefully noted the behavior of the tortoise while it was on the board, and recorded the time that it remained there. It would seem that the time from the noticing of the edge of the board till the fall should be recorded rather than the total time spent on the board, but as it was found that some species notice the spatial conditions while they are still in the middle of the board, whereas

others give no evidence of perception of the height until they have reached the edge, it was necessary to make the record as described. Since in these experiments it was necessary that time as well as space should be considered, 60 minutes was fixed as the duration of the experiment, and in case the animal remained on the board longer than that period the test was recorded as a failure. Failures in this case have positive value, to be sure, but they do not give us the accurate measurement of the time of reaction which indefinite prolongation of the period of observation would furnish.

For detailed study three species were chosen: *Chrysemys picta* Schneider, as a representative of the water inhabiting forms; *Nanemys guttata* Schneider, to represent those species which spend part of their lives in water and part on land, and *Terrapene carolina* Linnaeus, as a strictly land inhabiting form.

Several individuals of each of the species were studied. In the tables the results for four individuals of each are presented. Each individual was given one trial a day at each of the three heights, 30, 90 and 180 cm. for ten days. In Table I we have a summary of the results, which are given in detail for the various individuals in Table II. From an examination of the records the following facts appear: (1) The time spent on the board is shortest for the water species, longest for the land species. This indicates that the hesitation in the presence of a void increases as we pass from the strictly water forms to

TABLE I.

Reactions to Spatial Conditions of Tortoises of Different Habits.
Summary of Results.

	<i>Chrysemys picta.</i>		<i>Nanemys guttata.</i>		<i>Terrapene carolina.</i>	
Height.	Average Time.	Failures	Average Time.	Failures.	Average Time.	Failures.
30 cm.	0.57'	0	27.6'	11	42.7'	9
90 cm.	6.30'	0	49.1'	30	54.2'	33
180 cm.	10.10'	1	60.0'	40	59.2'	39

TABLE II.
Reactions to Spatial Conditions of
Chrysemys picta.

Subject No. 3.			No. 7.		No. 8.		No. 9.	
Height.	Average Time.	Failures	Average Time.	Failures.	Average Time.	Failures.	Average Time.	Failures.
30 cm.	0.37'	0	0.69'	0	0.74'	0	0.47'	0
90 cm.	12.80'	0	4.80'	0	3.10'	0	4.60'	0
180 cm.	17.50'	1	4.00'	0	2.30'	0	16.60'	0

Nanemys guttata.

Subject No. 1.			No. 2.		No. 3.		No. 5.	
30 cm	32.0'	5	9.4'	0	38 5'	5	30.4'	1
90 cm	60.0'	10	30.8'	4	53.6'	8	52.0'	8
180 cm	60.0'	10	60.0'	10	60.0'	10	60.0'	10

Terrapene carolina.

Subject No. 1.			No. 2.		No. 3.		No. 5.	
30 cm.	36.1'	0	38.1'	1	55.3'	7	41.4'	1
90 cm.	60.0'	10	40.7'	4	56.3'	9	60.0'	10
180 cm.	60.0'	10	56.8'	9	60.0'	10	60.0'	10

those which are land inhabiting; (2) Total inhibition of the reaction, i. e., failure to crawl over the edge of the board in the 60 minutes, appears at a much less height for the land species than for the water-land and water forms.

This quantitative expression of the amount of hesitation exhibited by different species of tortoises under the same spatial conditions clearly indicates a close relation between the demands of the natural environment of the species, so far as spa-

tial relations are concerned, and the behavior of the animals. A land tortoise has cause to notice heights and to react to them in a manner different from that of a water form. The former plunges over a precipice and is dashed to pieces, the latter plunges into the water from an equal height without injury. It is interesting to note, too, that there are intermediate forms between the two extremes, for the "spotted" tortoise *N. guttata* is more careful in its reactions to space than *C. picta*, but less so than *T. carolina*.

We may now turn from the roughly quantitative facts of this study to the observations of the general behavior of the animals when placed in unusual spatial conditions.

Of the three species of tortoises under consideration *Chrysemys picta* is the most active. At a height of 30 cm. it usually plunges off without hesitation; at 90 cm. it frequently stops at the edge, looks about carefully, and sometimes draws back and seeks another part of the edge. There can be no doubt that it senses the spatial relations in visual terms. At 180 cm. this species is manifestly afraid of the edge. Some individuals hesitate for long intervals before pushing off into space; others rush off at once. Usually, however, at this height the edge of the board is carefully explored, and abortive attempts to push off are made repeatedly. There is no evidence that the unusual conditions are perceived until the animal reaches the edge of the board.

Nanemys guttata hesitates even at the height of 30 cm. Most individuals carefully examine the board and look intently toward the net and surrounding objects before pushing off. They crane the neck over the edge to a greater extent than does *C. picta*. When 90 cm. or more above the net this species seldom approaches the edge without manifestations of fear. Frequently an individual pushes itself almost over, then stops suddenly and draws back, or attempts to catch the edge with its claws to save itself from falling. This striking conflict of impulses sometimes occurs repeatedly before the animal finally goes over the edge. The tortoise is impelled by the narrowness of its confines on the board, and by its isolated and exposed posi-

tion to seek escape, and, in the case of the water tortoises, to seek the water, but as it is pushing over the edge the visual impressions of distance initiate a conflicting motor impulse which causes the animal to draw back. This species manifests fear much more markedly, frequently, and at a less height than does *C. picta*. On the whole we may say that its behavior to spatial relations would ordinarily be interpreted as indicative of more accurate space perception.

At none of the three heights used in the experiments does *Terrapene carolina* push over the edge without some hesitation and manifestations of fear. At 30 cm. almost all individuals

TABLE III.

<i>Terrapene bauri</i> Taylor	Behavior much the same as that of <i>T. carolina</i> . There is careful inspection of the surroundings and long hesitation. One individual was found that plunged off directly at the height of 180 cm.
<i>Xerobates polpyhemus</i> Daudin	Examination of edge as in <i>T. bauri</i> . Hesitation at 30 cm., and great fear at 180 cm.
<i>Testudo vicina</i> Günther	Not afraid to fall 30 to 50 cm. but careful when at greater heights.
<i>Chelopus insculptus</i> Laconte	This species shows greater hesitation than does <i>N. guttata</i> . At 30 cm. it examines the surroundings, and often fails to leave the board.
<i>Emys meleagris</i> Shaw	In this species there is some hesitation at 30 cm. but seldom failure to go off. At 180 cm. there is marked fear as in <i>N. guttata</i> , which it very closely resembles in its behavior.
<i>Chelodina novaehollandiae</i> Dumeril et Bibron	Although this form carefully examines the edge and looks at the floor intently it seldom fails to go off. Its actions are very deliberate in most cases.
<i>Trachemys scabra</i> Agassiz	Many individuals pay no attention to the edge. Little hesitation even at 180 cm. Behaves much like <i>C. picta</i> .
<i>Podocnemis madagascariensis</i> Grandidier	No hesitation, no fear at any height at which it was tried. Pays less attention to spatial conditions than any of the species studied.

will leave the board if given plenty of time. This species is more careful than the others in approaching the edge, and it cranes the neck over even more frequently than does *C. picta*. The inhibition of impulses frequently appears as in case of *N. guttata*. Unlike the other species, *T. carolina* notices the spatial relations from its position in the middle of the board, for when 180 cm. above the net an individual is frequently afraid to move, and will remain for a long time just where the experimenter has placed it.

This study of the reactions to space of the three species of tortoises already considered was supplemented by observations of the behavior of several other species at the heights of 30 and 180 cm. In Table III, a summary statement of the results is presented.

Without knowledge of the name of the species, but solely on the basis of the results of the experiments, I classified the species under the three categories Water, Land-Water, and Land Species in order to determine the value of reactions to space as a sign of habits.

Classification in accordance with reactions to space.

Water Species.	Land-Water Species.	Land Species.
<i>Chrysemys picta</i>	<i>Emys meleagris</i>	<i>Terrapene bauri</i>
<i>Podocnemis mada-</i> <i>gascariensis</i>	<i>Nanemys guttata</i>	<i>Terrapene carolina</i>
<i>Chelodina novaehollandiae</i>		<i>Xerobates polyphemus</i>
<i>Trachemys scabra</i>		<i>Testudo vicina</i>
<i>Polymedusa galeata</i>		<i>Chelops insculptus</i>

This classification agrees fairly well with what is known of the habits of the forms, except that *Chelopus insculptus* is a land-water rather than a land species.

The Spatial Worth of Sense Data.

For the purpose of ascertaining the relative importance for reactions to space of the visual, tactual, muscular and organic sense impressions some experiments were made with blindfolded tortoises. The eyes, in these experiments, were covered with tin-foil caps which effectually excluded visual stimuli.

C. picta when blindfolded usually rushed off a surface at any height without the least hesitation. There is no evidence, from my experiments, that the tactual and muscular impressions received when the legs are stretched over the edge have any inhibitory influence on the movement. From this it is clear that the hesitation of this species observed at heights of 180 cm. is due to visual impressions, not to the unusual organic impressions received. This species at first tries to remove the covering from the eyes by rubbing the fore legs over the head, but failing it soon becomes accustomed to the blindfolded condition.

N. guttata is much disturbed by the obstruction of its vision, and for long periods persistently tries to remove the cap. Most individuals after a time move about freely, but whenever they reach the edge of the board they turn back." Evidently the tactual and muscular impressions inhibit the tendency to move forward. Whereas in case of *C. picta*, we see the blindfolded animal risking falls which it would not have risked in its normal condition, in *N. guttata* we see exactly the reverse, for as a rule the animal when blindfolded does not leave the board.

T. carolina does not struggle so persistently to remove the covering as do the other species, but it is inactive when blindfolded. It behaves in general much as it does when placed at a height of 180 cm. above the floor. This indicates that it depends upon vision for guidance in its movements to such an extent that it is not likely to move about much unless it can see clearly.

Visual impressions are of prime importance in the space perception of tortoises, and tactual, muscular and organic data occupy a position of secondary importance. Yet there are many reasons for believing that we often underestimate the value in the reactions of simple organisms of that complex mass of sense impressions which we are not as yet able to refer to specific organs. JAMES ('90, II, p. 150) has called attention to a fact that is significant in this connection; "Rightness and leftness," "upness and downness," he says, "are again pure sensations differing specifically from each other, and generically from

everything else." We are inclined to lose sight of the organic impressions, and to refer reactions to data received through the so-called special senses. Many experiments have already been made which show that the direction of turning, apart from vision, is extremely important in the motor habits of tortoises and frogs.

I gratefully acknowledge my indebtedness to Mr. SAMUEL HENSHAW for suggesting to me the desirability of a comparative study of the space reactions of tortoises; to Mr. THOMAS BARBOUR for valuable assistance in many ways, and for the opportunity of observing the behavior of several foreign species; to Mr. WM. T. HORNADAY, director of the New York Zoölogical Park, and to Mr. R. L. DITMARS, Curator of Reptiles, for the privilege of conducting experiments in the Park, and for many courtesies, and to Mr. C. W. HAHN for the use of tortoises which were in his possession.

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A NOTE ON THE SIGNIFICANCE OF THE FORM
AND CONTENTS OF THE NUCLEUS IN THE
SPINAL GANGLION CELLS OF THE FOETAL
RAT.

By SHINKISHI HATAI.

(From the Neurological Laboratory of The University of Chicago.)

With Plates III and IV.

In the course of an investigation on the growth changes in the nerve cells of the white rat, the writer noticed that the nucleus very often had a peculiar shape; the shape being similar to an amoeba exhibiting pseudopodia-like processes along one side. Careful observation revealed the fact that this peculiar form of the nucleus occurs normally during the period of the early growth and in attempting to explain it we meet several interesting questions of histological as well as physiological importance. The results here reported form a part of a series of observations on the growth changes in the developing nerve cells.

For this investigation, the intrauterine embryos of cat, pig and white rat were used. The present description and drawings are, however, based entirely on preparations from white rat. Unless otherwise mentioned, the description also applies to the cat and pig. The tissue was preserved in a normal salt solution saturated with HgCl_2 ; in CARNOY'S solution and in GRAF'S chrom-oxalic mixture. For the microchemical test for P. and Fe., however, the tissue was fixed advantageously with 95% alcohol. The paraffine sections were made 3 to 6 micra in thickness, and were stained with HEIDENHAIN'S iron-haematoxylin alone or sometimes followed by 1% aqueous solution of eosin and BIONDI-EHRlich's tri-color stain. Other sections were stained with toluidin blue and eosin.

General characters of the spinal ganglion cells.—The spinal ganglion cells in embryos of the white rat, 10 to 13 mm. long, present a bipolar shape in most cases; one of the processes contains a large amount of the cytoplasm and is recognized easily because it stains more deeply than the other. The second process arises from the opposite side of the cell-body and stains faintly. It contains a very small amount of cytoplasm and is hard to distinguish from the surrounding structures. Only the former process is shown in the figures. The relation of these processes to the spinal cord will be described in a future paper. Hereafter, in this paper, the term process means the former branch, rich in cytoplasm.

The nucleus is very large compared with the cell-body and presents a more or less oval shape. It contains a large number of the minute granules among which two different forms may be distinguished, not only by their size but also by their staining reactions with iron-haematoxylin; one form of the granules stains deep black while the other presents a grey tint. The granules which stain an intense black are very much larger in size and occur most abundantly along the nuclear wall and its vicinity; the faintly staining granules, on the other hand, are very small in size and appear to form a fine network in the nucleus. This network is most condensed around the larger granules of the former group. The large granules are identified with the basophile substance and the small granules with linin or oxyphile substance. This grouping is by no means satisfactory, for by using the BIONDI-EHRLICH stain, as well as by applying the microchemical tests, it has been noticed that among basophile granules (larger form) there are several different kinds which stain with different intensities and similarly there are several different kinds of the oxyphile granules. So far, therefore, as color reactions are concerned, the oxyphile and basophile granules grade into one another and no sharp distinction can be drawn between the two. This fact is extremely important in connection with the present investigation and will be discussed more fully later on.

Among the large granules, sometimes one and in some

cases more than one, can be distinguished as exclusively composed of the basophile substance, but in many cases, the large granules contain both basophile and oxyphile substances. When this occurs and the basophile surrounds the oxyphile substance then such a granule may be regarded as a nucleolus of the adult nerve cells.

Enlarged granules of this nucleolar type are shown in Figs. 1 and 2. The position of these granules is not constant but they lie in some cases along the nuclear membrane and in others they occupy the center of the nucleus (Fig. 1).

Shape of nucleus.—Changes in the shape of the nucleus and the alterations of its position in the cell have been noted by a number of observers. The phenomena have been observed especially under experimental and pathological conditions. In the normal condition, however, they have been reported by only a few investigators. Several investigators observed a pocket formation along the nuclear surface in the spinal ganglion cells of fish. These invaginations are repeated several times in one nucleus, some of them being deeper than the others, and thus the nucleus presents pseudopodia-like processes. Such an appearance is rather common in the nuclei of the nerve cells in spinal ganglia and ventral horn of lower vertebrates (HOLMGREN), but on the other hand, it is rarely visible in the cells of the higher mammalia, and when it occurs it is not so conspicuous as in the lower forms. The present writer had the opportunity to examine a large number of the preparations of the nerve cells of the white rat at different ages, but failed to find the pseudopodia-like processes of the nuclei in animals of one day or older. As a rule, after the age of one day the shape of the nuclei is constantly ovoid or spherical and does not show pseudopodia-like processes.

By examining the nuclei of spinal ganglion cells of embryos (10 to 13 mm.), the following appearances have been observed:

As is shown in the figures, the nucleus of the embryonic spinal ganglion cells lies, as a rule, at one side of the cell body; that is it lies eccentrically. Such an eccentric location of the

nucleus also occurs in the cells of the adult animal. The shape of the nuclei is somewhat oval, the longer diameter being perpendicular to the long axis of the protoplasmic process. On one side towards the center of the cell, the outline of the nucleus is more or less wavy. In some cases, the wavy outline is not very marked (Fig. 5) but in most cases, it is conspicuous and one is lead to compare it to the pseudopodia-like process of an amoeba (Figs. 1, 2, 4).

The nuclei showing the pseudopodia-like processes have been observed by several investigators; in the egg nuclei of the insects and Coelenterata by KORSCHULT ('89); in the spinning gland cells of a Swedish caterpillar and also in the spinal ganglion cells of the fishes, frogs, etc., by HOLMGREN ('95-'00); in the developing ovum of the *Nassa* by HOFFMANN ('02); in the nuclei of the ventral horn cells of various vertebrates by KOLSTER ('01); and the same thing is also shown in the illustrations accompanying a large number of papers in which, however, the authors do not describe this interesting phenomenon. Before going on to a further discussion of this appearance, I shall describe more in detail the histological characters of the wavy outline together with the structure of the adjoining part of the cell body which contains the centrosome.

The nuclear membrane which covers the pseudopodia is not completely continuous but is composed of separate portions when seen in thin sections; in other words, the surface of the nuclear membrane towards the cytoplasm is porous. A disappearance or dissolution of the membrane on this side of the nucleus has been observed by HOLMGREN, and PUGNAT ('98), but in the case of the white rat, it is always porous in character. This is clearly shown in Fig. 2. In many cases, however, the local dissolution of the nuclear membrane is not as conspicuous as in Fig. 2, but the outline appears varicose in structure owing to an accumulation of basophile granules around the pores (Figs. 2, 5).

The nuclear membrane which lies towards the protoplasmic process is of uneven thickness. The thicker portions stain much more deeply than the rest of the membrane with the

basic dyes (Figs. 1, 5). This indicates that the thicker portions contain an accumulation of the nucleoproteid. This statement is supported by the fact that the preparations tested for iron show this area deeply stained (Fig. 2). The accumulation of the nucleoproteid along the part of the nuclear membrane which turns towards the process is a highly interesting phenomenon since it bears on the problem of the cell metabolism. This point will be discussed later on in detail. An accumulation of the nucleoproteid is frequently visible along the outer surface of the nuclear membrane as is shown in Fig. 3.

These pseudopodia-like processes of the nucleus are intimately related to the rays of the centrosome. The centrosome in nerve cells has been described by several investigators, and in the nerve cells of the white rat in both adult and young it has been described by the present writer ('01). Although some investigators deny the existence of the centrosome in the nerve cell, the structure is so definite and so clear that in properly prepared sections, its presence can not be disputed. The centrosome is especially clear in the case of the embryonic cells and every minute feature of the organ may be distinguished. As a rule, the centrosome lies very near the nucleus and in the concavity formed by it (Figs. 1, 2, 3, 4, 5). The centrosome is composed of two minute central corpuscles surrounded by still more minute granules (centrosphere). These granules arrange themselves in straight lines which run from the center towards the periphery radially (astral lines). The astrosphere is clearly distinguished from both surrounding cytoplasm and centrosphere, since it stains very lightly with iron-haematoxylin owing to a lack of the NISSL granules. By overstaining with acid dyes, however, astrosphere stains a more intense red than the surrounding substance. The minute structure of the centrosome in the nerve cells of the white rat has been reported already by the writer ('01) and therefore, with the exception of the astral structure, it need not be further described here. The astral rays which start from the centrosphere run radially towards all parts of the cell body. Those rays which runs towards the nucleus extend not only as far as the nucleus but penetrate its

membrane and become directly continuous with the linin network. This is shown in Figs. 1, 2, 4, 5. As is shown in the figures, the protoplasmic lines pass through the pores of the nuclear membrane and run into the nucleus where they fuse with the linin network. Some of the rays fuse together with the linin network as soon as they enter into the nucleus, but others run quite a distance without losing their original character as rays. Ultimately, however, they fuse with the network and no rays can be seen near the periphery of the nucleus. The penetration of these rays was verified by careful examinations, many times repeated, all precautions being taken against possible mistake. Thus my observations on the spinal ganglion cells of the white rat show a direct continuation of the cytoplasm and nuclear network by means of the rays of the centrosome. In addition to these observations, HOLMGREN ('99) noticed in adult nerve cells of *Lophius piscatorius* that the NISSL granules were hung along the astral rays and that these granules could be traced with them into the nucleus. From this fact HOLMGREN concluded that the NISSL granules are formed by the migration of the chromatin out of the nucleus, and that the granules thus formed are again passed back into the nucleus by means of the rays. He, therefore, regards the rays as a pathway by which NISSL granules re-enter the nucleus. The present writer was unable to find any formed NISSL granules along the line of the rays within the centrosphere. Therefore the returning of the formed NISSL granules into the nucleus was not found in the nerve cells of the white rat. I will return to this point in general discussion.

Distribution of the nuclear material.—At this stage of intra-uterine life, the nucleus of the nerve cell contains a large number of the chromatic particles which are scattered through it. The particles vary in size from minute granules to comparatively large bodies. The larger granules do not exceed five in number and may be composed exclusively of basophile substances. Subsequent to the stage in which basophile and oxyphile granules are distinct, the nucleolus appears. The minute granules as distinguished from large granules, mentioned above, stain

with iron-haematoxylin a deep black to a grey. The iron test shows in the same granules also varying amounts of the iron. These granules are hung along the linin net as is shown in all the figures. By using BIONDI-EHRLICH's tricolor stain, these granules stain from a deep blue to a brownish red; thus all the staining methods employed show that these granules are chemically heterogeneous. This gradation in the staining capacity probably indicates gradations in the chemical constitution of the granules which range from a substance rich in nucleic acid to a substance poor in nucleic acid. These granules are found most abundantly along the nuclear membrane, especially at the two poles of the nucleus on the side toward the cytoplasmic process (Figs. 1, 4, 5). It is a striking fact connected with the distribution of the granules that the appearance of the NISSL granules in the cytoplasm is clearly correlated with the accumulation of the granules at the two poles of the nucleus. The NISSL granules first appear in the neighboring cytoplasm. This fact suggests that the NISSL granules are derived from the nucleus.¹ From facts similar to those just given, as well as from other evidence, SCOTT ('98-'99) arrived at the conclusion that the NISSL granules are of chromatic origin and are produced by the migration of the basophile granules from the nucleus. The nuclear origin of the nuclein compounds which are seen in the cytoplasm has been maintained by several investigators from observations on glandular tissues as well as on the muscles. My own observations therefore indicate the nuclear origin of the NISSL granules and thus corroborate the observations of these previous investigators, HOLMGREN ('99) on the nerve cells of *Lophius piscatorius* and ROHDE ('03) on the nerve cells of various vertebrates.

¹ The formation of the NISSL granules in the nerve cells is comparable with the formation of the zymogen granules, muscle fibrils, and yolk granules. This is a highly important and fundamental problem in cellular biology and the subject is fully discussed and presented historically in WILSON's "Cell in Development and Inheritance," 2nd edition, 1900.

*Migration of the nucleoli.*¹—A migration of the nucleolus as well as other nuclear material from the nucleus to the cell body has been reported by several investigators. In the case of the nerve cells, ROHDE ('96-'03) observed the migration of the nucleolus in the case of both lower vertebrates and mammals. In a recent paper on the nerve cells, ROHDE ('03) maintains the migration of the basophile substance from the nucleus, where it exists in solution, into the cytoplasm. LEVI ('96) believes the neurosomes in the cytoplasm to be derived from the nucleus. LEVI showed this relation by the electrical stimulation of nerve cells. In the present work, I have noticed also the migration of the nuclear substance or accessory nucleoli from the nucleus to the cytoplasm. This is so often seen in the nerve cells at this stage of development that it cannot be regarded as an artifact. The migration is always towards the cytoplasmic process, no matter whether this process turns distally or toward the spinal cord. If the dislocation of the large masses or accessory nucleoli were due to mechanical forces, the knife or gravitation, or to other mechanical factors, one would expect to see them moved towards the less resistant side, that is towards uncovered side of the nucleus, as in the case of pathologically altered cells in which the nucleolus or intranuclear masses escape towards the side on which the cytoplasm is least abundant. Again, if such a migration were produced by the knife or gravitation, as HERRICK ('95) showed to be the case in the ovarian cells of the lobster, one would expect to find the displacement always in the same direction in all the cells of a given section, but such is not the case. Moreover, the general appearance within the cells does not suggest a mechanical bursting of the nuclear membrane. For these reasons, I believe that the observations of ROHDE and others are correct and my own observations strongly confirm their statements. The fate of the extruded granules has still to be considered. In order to

¹ History of the observations on this subject in the tissue cells is given in detail by MONTGOMERY, T. H.—Comparative Cytological Studies with especial regard to the Morphology of the Nucleolus, *Journ. Morphology*, VOL. 15, No. 2, 1898.

understand their final destination it is necessary to describe the migration of the nuclear substance more in detail. Figures 4, 5, 6, 7 and 8 illustrate this. The granules, for the most part accessory nucleoli, may be both larger and smaller than the other granules contained in the nucleus. They stain deep black with iron-haematoxylin and rather pinkish red with the tri-color method; that is, their staining reaction resembles very closely that of the Nissl granules. These accessory nucleoli, therefore, can be distinguished from the nucleolus since the latter is composed of the two substances, basophile and oxyphile. In each case I noticed only one granule migrating at a time, although I have seen once or twice several granules attached along the external surface of the nuclear membrane on the side toward the process (Fig. 3). This arrangement is very rare and cannot be regarded as typical. The migration always takes place towards the main protoplasmic process and in addition the granule is extruded in the neighborhood of the poles of the nucleus where the Nissl granules first appear. After migration I was unable to see these granules at any distance from the nucleus, though they were abundant near to it. From this we conclude that as soon as the granules migrate from nucleus, they disintegrate and their substance is mixed with the surrounding cytoplasm. If the corpuscles which have migrated out of the nucleus still continue their movement until they finally come out of the cell body, as is believed by ROHDE, it would be possible to observe such corpuscles outside of the cell body, but I have not been able to find them. Therefore from at least three facts: (1) that the granule after migration is always found near the nucleus; (2) that the granule after migration is not found in the cytoplasm at any distance from the nucleus and (3) that it is not found outside the cell body, the writer concludes that these granules have been disintegrated and mixed with the surrounding cytoplasm. If my hypothesis is correct the migration of the accessory nucleoli is another form of the extrusion of the minute granules; a second form of the nuclein formation in the nerve cell—the first or commonly rec-

ognized method being the extrusion of very small granules. (See page 33).

Judging from the staining reaction of the accessory nucleoli which contain both phosphorus and iron, they are composed of the same substance as the NISSL granules and therefore it may be safely concluded that the disintegrated substance was utilized for the formation of the NISSL granules. This observation agrees with that of ROHDE, but with his further statement that some of the accessory nucleoli become the neuroglia nuclei, I cannot agree. So far as my observations on the nerve cells of the white rat go, there is no indication that the accessory nucleoli form the nuclei of the neuroglia cells. The migration of the accessory nucleoli was found only in the cells at the early stage of intra-uterine life here examined, and at more advanced stages I was unable to observe this phenomenon, although a number of later developmental stages were studied. From this fact, we may conclude that extrusion of the nuclear substance into the cytoplasm occurs only in the very early stages of the developing nerve cells.

Significance of the pseudopodia-like processes of the nucleus.—The observations of the previous investigators (HOLMGREN, ROHDE and SCOTT), as well as those presented in this paper, furnish good evidence for believing that NISSL granules originate in at least two ways; namely (1) by the extrusion of small granules; (2) by the extrusion of accessory nucleoli. If all the materials which appear in the NISSL granules of the mature nerve cell are derived from the chromatin of the nucleus, then it is plain, since the nucleus at no time contains as much substance as is presented by the NISSL granules at maturity, that the chromatin of the nucleus must be continually built up by the material supplied to it from the cytoplasm. So far as I am aware no investigator except HOLMGREN ('99) has attempted to explain this phenomenon. HOLMGREN found in the nerve cells of *Lophius piscatorius* that the NISSL granules are hung along the astral rays which run through the nuclear membrane and according to him this indicates the return of the NISSL granules to the nucleus by way of the astral rays. Thus, according to him,

there is a circulation of the NISSL granules between the nucleus and cytoplasm. In the general description of the nerve cell, my results agree with those of HOLMGREN in the following points: (1) the rays of the attraction sphere run into the nucleus where they become continuous with nuclear network, (2) the NISSL granules migrate from the nucleus either as minute granules or accessory nucleoli, (3) the nuclear membrane becomes perforated along the surface which turns toward the cytoplasmic processes. However, I was unable to see the basophile granules either within the centrosphere or along the astral rays in the cytoplasm. Therefore, HOLMGREN's hypothesis of the return of the formed NISSL granules into the nucleus is not supported by the appearances in the nerve cells of the white rat. My own observation suggests that the NISSL granules which have migrated from the nucleus are utilized for the maintainance of the cell body and what remains of them after they are broken down, together with fresh material, is taken into the nucleus by means of the pseudopodia-like processes. For the above view, the following evidence may be presented:

(1) The pseudopodia-like processes of the nucleus are directed towards the central corpuscles of the centrosome. According to KORSCHULT ('91), HOFFMANN ('03) and others the pseudopodia-like processes are to be regarded as organs taking up nourishment from the surrounding cytoplasm.

(2) In them, as well as in their vicinity, basophile granules are abundant.

(3) Within the nucleus, the astral rays are surrounded by, or have attached to them, a large number of basophile granules.

(4) Positive proof of the presence of iron and phosphorus was obtained in the granules along the rays, as well as within the centrosphere, although they did not give with HEIDENHAIN's iron-haematoxylin nor with the tricolor methods reactions similar to that produced in the NISSL granules. This proves that the substances necessary for the formation of the nuclein bodies (NISSL granules) are present in the centrosphere as well as in its rays, in a peculiar form.

As supplementary to the foregoing the following observations may be added: (1) the pseudopodia-like processes of the nucleus as well as the migration of the accessory nuclei are present only at a very early stage in the development of nerve cells, at the time when the NISSL granules have not yet appeared or are found in very small amounts, and when the cell body needs an abundant supply of formative materials. The pathological as well as experimental studies give us still stronger evidence for the foregoing view.

Pathological and experimental evidence.—The morphological completeness of the cell body is attained in an early foetal period when metabolic processes in the cell body are very active and we associate the formation of pseudopodia-like processes and the migration of accessory nucleoli and of the minute granules, with the hyperactivity of the cell at this time. The experimental studies of the nerve cells made by a large number of investigators (HODGE, '92; MANN, '95; SJÖVALL, '03; and others) show that when the nerve cell is stimulated with the electric current, the nucleolus becomes first swollen and later shrunken; the outline of the nucleus becomes irregular, forming pseudopodia like processes (HODGE, see figures); accessory nucleoli migrate out of the nucleus (HOLMGREN); acidophile substance or neurosomes are sent from the nucleus into cell body (LEVI); at the same time the NISSL granules are quickly disintegrated. These observations favor my hypothesis of the metabolic processes in the cell since they are similar to those changes which take place normally at an early stage in the history of the cell body when it is actively growing. As a result of the electric and other stimulation the reserve materials of the NISSL granules are used up very quickly and for the maintenance of the cell a new supply of the substance is demanded. The migration of the nuclear contents and the quick absorption of the necessary materials from the cell body into the nucleus by means of the pseudopodia-like processes are both necessary. Notwithstanding that a large number of investigators have examined the nerve cells under various conditions, the pseudopodia-like processes have been overlooked by most of them.

SJÖVALL ('03) has pointed out these structures in the human nerve cells, in a patient dying from tetanus, and gave many figures showing different stages of the processes of the formation of the granules. SJÖVALL showed further an accumulation of basophile granules along the nuclear membrane where the processes are covered. He concluded from these observations that "Die gesehenen Veränderungen sind als von der tetanischen motorischen Erregung verursachte, innerhalb völlig physiologischer Grenzen sich abspielende Aktivitätserscheinungen aufzufassen, und nur als solche. Zu dieser Ansicht komme ich: (1) Weil sie den experimentell hervorgerufenen Aktivitätsveränderungen der Nervenzellen wesentlich gleich sind. Dies betrifft; (a) sowohl die früher gesehenen Veränderungen, (b) wie die von mir gefundene Beziehung zwischen Kern und Protoplasma, die mit den Befunden von HOLMGREN identisch ist, und, wie diese, sicher als einen Restitutionsvorgang des während der Aktivität in anspruch genommenen Tigroids zu deuten ist."

The writer had a chance to examine several preparations of the nerve tissue of rat, cat, dog and man under pathological as well as under experimental conditions and found always the pseudopodia-like processes at one side of the nucleus. This phenomenon was more clear when the nucleus was located eccentrically; the pseudopodia being extended toward the main portion of the cell body. These observations show changes in the cell body and nucleus corresponding to those occurring during foetal life.

Growth changes in the nerve cells.—As soon as the pseudopodia-like processes have disappeared marked changes take place in the structure of the nucleus. The most notable changes are: (1) the nucleus assumes a spherical or oval shape with a smooth outline; this shape is maintained during life; (2) the chromatic granules (basophile) which existed abundantly along the nuclear membrane disappear and at the same time some of the granules move towards the center where they surround a cluster of the acidophile granules and form a permanent nucleolus; (3) most of the basophile granules are changed into oxyphile granules as is shown by the change in staining capacity, since the orig-

inal basophile granules are now stained with acid-dyes; (4) following the nuclear changes just described the cell body is filled with the basophile granules or the NISSL substance; (5) the astral rays of the centrosome are not as clearly shown as in the earlier stages. The nerve cells thus changed do not differ from the adult functional cells except in size and, therefore, it may be concluded that the morphological completion of the nerve cell of the white rat is attained during early intra-uterine life. In the case of man, MARINESCO ('99) and BIERVLIET ('00) noticed such fully formed NISSL granules in the ventral horn cells of the spinal cord at birth. This does not mean, however, that all the NISSL granules are formed in the cells at this stage, but that they are relatively as abundant as in the adult cells. Therefore it is clear that when the cell body increases in volume the amount of the stainable substances increases correspondingly. The explanation of the formation of the stainable substance at the latter stage is not easy, since at this stage the structure of the nucleus is different from that of the earlier stage in which the nucleus resembles that which can be seen in the cells of the active glandular tissue. Before going into a further discussion of this point, it will be well to describe the main features of the nucleus in the adult nerve cells.

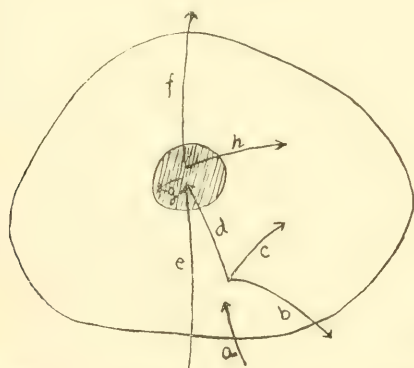
The nucleus in the spinal ganglion cells.—The nucleus in the spinal ganglion cells in an adult white rat is slightly oval in shape and is located at or near the center of the cell. The nuclear membrane is very distinct and can be distinguished easily from the surrounding cytoplasm. The nucleolus appears nearly in the center of the nucleus, consisting as a rule of a single corpuscle and staining an intense blue with toluidin blue and erythrosin. Several endonucleoli are often distinctly visible within the nucleolus. These are composed of acidophile substance. The nucleolus is, therefore, composed of two different substances, acidophile substance within, the basophile substance without. The nucleus contains a linin network and a large number of the acidophile granules; the latter hung on the threads of the former and most abundant along the periphery of the nuclear membrane and around the nucleolus. Thus, except the baso-

phile covering of the nucleolus, no more chromatic substance can be demonstrated by using ordinary stains like toluidin blue and erythrosin. It is a well-known observation, not only in the early embryonic nerve cells but also in the cells of the active glandular tissues, that preceding the migration of the chromatic substance from the nucleus to the cell body the substance appears at first along the inner surface of the nuclear membrane whence it passes by either diffusion or migration into the cytoplasm. But as described above, the nucleus of the adult nerve cell does not show basophile or chromatic substance except as in a thin layer about the nucleolus.

Very recently, by applying ZIMMERMANN'S "Jodgrünfuchsin method" to the nerve cells in various animals, ROHDE ('03) arrived at the conclusion that "Das Enchylema ist färbbar und zwar durch Jodgrünfuchsin wei die Nukleinkörper. Es enthält demnach ebenfalls Nuclein, entweder gelöst oder in diffuser Form." This conclusion is correct also in the case of the white rat. I applied the iron and phosphorus reaction to the adult nerve cells and obtained always positive results from the enchylema which, however, does not stain by using ordinary histological technique. Figure 7 is a drawing of the ventral horn cells in an adult white rat treated by the method for detecting iron and phosphorus. As the figure shows, the NISSL granules are directly continuous with the dissolved nuclein in the nucleus. At the two poles of the oval-shaped nucleus, the dissolved nuclein is most abundant (Fig. 7) and from these poles it diffuses out of the nucleus into the cytoplasm. By using the technique for phosphorus and iron one is surprised to see the large amount of the nuclein which exists in a soluble condition. Thus one can easily imagine a cyclical interchange of the substances between the cell body and nucleus, since the material to be exchanged is in solution in the enchylema. The application of technique for the detection of phosphorus and iron to the spinal ganglion cells in the adult rat shows the same results and therefore does not need to be especially described. These appearances suggest that in the adult and later stages the NISSL granules are formed in the cytoplasm from the nuclein

which has diffused out of the nucleus. This hypothesis is favored by examining the adult nerve cell which has been stained either by toluidin blue and erythrosin or by HEIDENHAIN's iron haematoxylin, followed by orange G. These stains show minute particles densely packed around the nucleus; especially at its two poles. This appearance is shown in figure 8, which has been drawn from one of the adult ventral horn cells stained with iron haematoxylin. As is shown in the figure, densely packed minute granules appear around the nucleus. Some of the granules stain a deep black, while the rest of the granules are tinged grey. Now if we apply the test for phosphorus and iron to such a preparation, the peripheral layer of the nucleus just within the membrane is found packed with a large amount of the dissolved nuclein, as is shown in figure 7, but is not shown in figure 8. From these figures we conclude that the dissolved nuclein which does not take up either toluidin blue or iron-haematoxylin has been modified into a stainable form on passing from nucleus. This change is due perhaps partly to the accumulation of the minute granules into comparatively larger granules and partly to a chemical transformation of the dissolved nuclein into the true NISSL granules. SCOTT ('99) was able to distinguish three different kinds of the nuclein compounds in the nerve cells; NISSL granules, basophile granules or covering substance of the oxy-center or the central mass of the nucleolus, and oxychromatin. According to him, these three nucleins were derived from the mitotic chromatin of the primitive nerve cells (germ-cells). It must be kept in mind that all substances in the body are undergoing constant metabolic change. Further, the NISSL granules increase in proportion as the oxychromatin increases with the growth of the cell body. This means that a new formation of the NISSL granules takes place within the cell body constantly; that is, katabolic and anabolic processes are going on incessantly. The play of these two processes within the cell body is beautifully described by MAX. VERWORN ('99). He says "The cell receives certain substances from the outside; of these some (a) upon meeting substances already present in the protoplasm,

undergo decomposition and synthesis. Of the substances resulting from these transformations some (b) are at once excreted as useless, others (c) remain in the protoplasm and are there employed further, while a third class (d) is passed on to the nucleus. The nucleus, moreover, obtains a portion of the substances (e) received from the outside and passed on unchanged through the protoplasm. The substances (d+e) entering into the nucleus there undergo on their part certain transformations, from which again substances result; these in part (f) are given off to the outside without being changed by the protoplasm, in part (h) pass to the protoplasm to find there further employment, and in part (g) remain in the nucleus itself. If, now, we realize that every arrow represents a sum of substances, that the substances passing from the nucleus to the protoplasm undergo transformations as well as those entering from the outside, and that the substances arising from these transformations are in part conveyed again to the nucleus, we obtain an approximate idea of how close the metabolic connection of the nucleus with the protoplasm is."



Text-figure 1. Scheme of cell-metabolism (VERWORN)

All these changes illustrated by VERWORN may be traced also within the nerve cells. It is, however, always difficult to correlate physiological phenomena with histological structure, but from the present studies on the nerve cells, sufficient evidence has been obtained to make some application of the histological facts to the physiological phenomena in the nerve cells.

For instance, as I have already mentioned, in an earlier stage of the cell life, the first NISSL granules are derived from the nucleus either by diffusion or extrusion, some of them changed, while others remain unchanged. The changed granules are utilized in part for the formation of the cytoplasm and in part during this process are returned to the nucleus or excreted as waste. While in the adult nerve cells, the dissolved nucleins are transformed into the NISSL granules, ground substance, pigment, oxyneutrophile granules (MARINESCO, '02), amphophile granules (OLMER, '01), neurosomes (HELD, '95), etc. All the structures given above differ from one another morphologically as well as chemically, thus indicating that the nucleins in the nucleus, after they have been brought into the cytoplasm are transformed there. This corresponds with the scheme of VERWORN.

SUMMARY.

The following is a summary of the main facts given above :

(1) At a very early stage of the spinal ganglion cells of the white rat, pseudopodia-like processes are formed from the nucleus and extend towards the protoplasmic process. The membrane of the pseudopodia is perforated.

(2) Through these perforations the astral rays of the centrosome, which lies near the nucleus and is enclosed by the pseudopodia, penetrate into the nucleus and become continuous with the linin network.

(3) The NISSL granules, when first formed, are derived either by the diffusion of the nucleins from the nucleus or by a migration of the accessory nucleoli into the cytoplasm.

(4) The materials for the formation of the nuclein are absorbed into the nucleus by means of the pseudopodia. These materials are collected from the periphery of the cell body to the center of the centrosome by means of the astral rays and then again through these rays they are conveyed toward the pseudopodia.

(5) At an advanced foetal stage, as well as in the adult, the nucleins are enclosed within the nucleus in a dissolved con-

dition, as is shown by the technique for the detection of P. and Fe. These nucleins pass into the cytoplasm by diffusion. The diffusion occurs most actively from the two poles of the oval nucleus.

(6) The changes in the nerve cells in pathological conditions or after excessive stimulation may be regarded as the result of hyperactivity since similar changes are observed normally in the cells during the period of most active growth.

(7) A return of the NISSL granules as such from the cell body to the nucleus by means of the astral rays (HOLMGREN) was not observed in the case of the white rat.

(8) A formation of the neuroglia nuclei from the migrated accessory nucleoli (ROHDE) was not observed.

(9) There is not the slightest evidence to favor the recent theory presented by KRONTHAL, who believes that the nerve cells are built up from leucocytes.

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EXPLANATION OF THE FIGURES.

The following figures are free-hand drawings using ZEISS Oc. 4+Obj.

1-12.

a, centrosome; *b*, amoeboid processes; *c*, basophile granules; *d*, acidophile granules; *e*, accessory nucleolus.

Fig. 1 to Fig. 6, Spinal ganglion cells of foetal white rat.

Fig. 7 and Fig. 8, Cells in ventral horn of adult white rat.

PLATE III.

Fig. 1, Stained with BIONDI-EHRlich's tricolor.

Fig. 2, Treated with MACALLUM'S technique which shows the distribution of iron.

Fig. 3, Stained with BIONDI-EHRlich's tricolor.

Fig. 4, Stained with HEIDENHAIN'S iron-haematoxylin.

PLATE IV.

Fig. 5, Stained with BIONDI-EHRlich's tricolor.

Fig. 6, Stained with BIONDI-EHRlich's tricolor.

Fig. 7, Treated with MACALLUM's technique which shows the distribution of phosphorus.

Fig. 8, Stained with HAIDENHAIN's iron-haematoxylin.

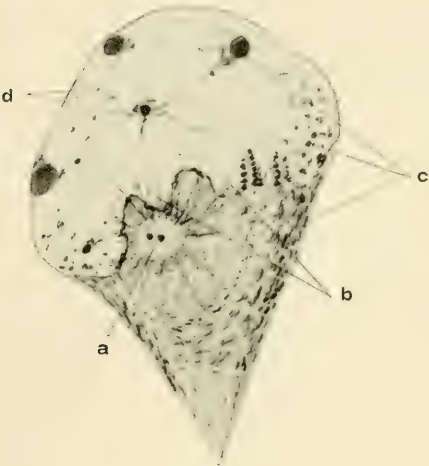


Fig. 1

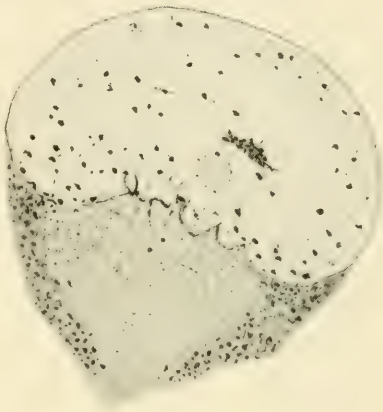


Fig. 2



Fig. 3



Fig. 4



Fig. 5

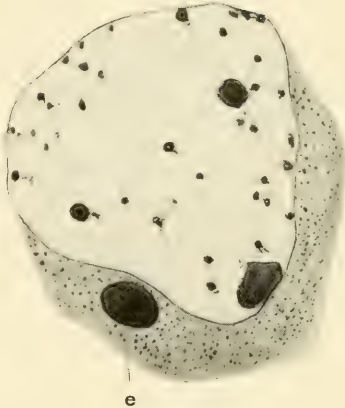


Fig. 6

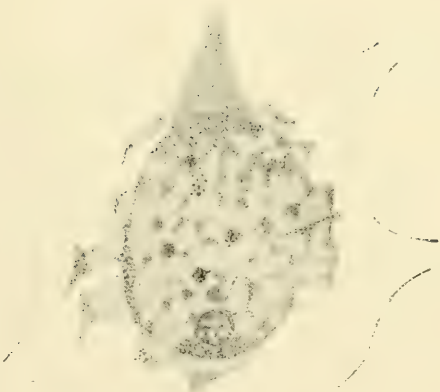


Fig. 7

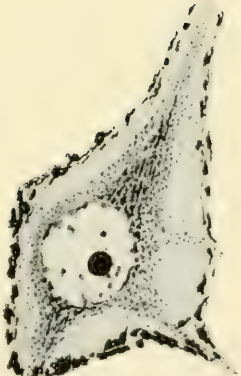


Fig. 8

AN ESTABLISHMENT OF ASSOCIATION IN HERMIT CRABS, EUPAGURUS LONGICARPUS.

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Introductory.

The experiments described in this paper are the result, first, of preliminary observations of a number of hermit crabs kept for some time in an aquarium at the Woods Hole Laboratory, which showed them to be quite capable of profiting by experience. In fact, the results first obtained were in general quite confirmatory of those obtained by the subsequent more systematic investigation, the method for which they indicated.

BETHE¹ and YERKES² have each made experimental studies of habit formation in the Crustacea, the former on the crab, *Carcinus moenas*, the latter on the crawfish, *Cambarus affinis*, and on the green crab, *Carcinus granulatus*. BETHE at the end of his paper relates some experiments made to determine whether or not the crab possesses psychical processes, with the result that he asserts that it does not. This conclusion is not, however, necessarily to be accepted even from BETHE's own experiments, for the reason that these at best serve to demonstrate the absence of only *one kind* of psychical phenomena, viz., those of inhibition or control; other kinds may be present. BETHE himself does not recognize that the method he employed was defective in this respect, but an account of it will, we think,

¹ BETHE, A., Das Centralnervensystem von *Carcinus moenas*. *Archiv f. mikr. Anat.*, Bd. 51, 1898.

² YERKES, ROBERT M. and HUGGINS, GURRY E. Habit Formation in the Crawfish, *Cambarus affinis*. *Harvard Psychological Studies*, Vol. I. 1903.

YERKES, ROBERT M. Habit Formation in the Green Crab, *Carcinus granulatus*. *Biolog. Bulletin*, Vol. III. 1902.

make evident the justification of our criticism. His *first* experiment was to place a crab in a basin in the darkest corner of which there was an *Eledone* (a cephalopod). The crabs, because of their instinct to hide, moved immediately into this corner and were seized by the *Eledone*. Freed from its grasp one crab returned repeatedly five times, another six, to the dark *and the enemy*, showing, as BETHE thinks, that it had not profited by experience. It is to be emphasized, however, that to have done this latter in the way BETHE thought possible, it would have been necessary that the crab *inhibit* its instinctive action. This inhibition could take place only if, first, a *representation* of the pain of the seizure by the *Eledone* were present, and second (and essentially), if the *representation* were the "*stronger*"; the other possibility, that the representation should occur and yet be overcome by the instinct, is accordingly not disproved by BETHE's experiment. The same criticism applies also to his second method that, notwithstanding maltreatment on each such occasion, the crabs repeatedly seize food when offered.

The criticism above made is quite in agreement with that principle of method for comparative psychology which is in reality very simple, but not always observed, that in any instance where the question of the presence of consciousness in any species is *admittedly* to be decided by experimentation, this question must take a *particular form*, and our efforts must be directed to the establishment of the presence or absence of some definite kind of consciousness, e. g., associative memory between constructs of two sense fields, conceptual reasoning, etc.

YERKES in his experiments with the crawfish made use of the labyrinth method. The subject could escape from a box into the aquarium only by "choice of a certain passage." The "choice" consisted in or was manifested by learning (by repeated experience) to avoid the blocked passage and gain the aquarium by the most direct path. Accordingly all conflict, requiring inhibition, between the two elements or "constructs" to be associated, viz., "correct path" and "aquarium," was ab-

sent. "Correct path," as opposed to the incorrect, logically implies in these experiments "aquarium"; and its selection, as shown by the ratio of improvement from day to day may, though not necessarily, imply the representation of the construct "aquarium," but it does demand the admission that acts of recognition and discrimination, or even of what LLOYD MORGAN calls "perceptual inference" take place. These in turn presuppose necessarily, as is well known, retention and production.

Carefully excluding the possibility of the crab's merely following a path by smell, taste, or touch (although if it did *only this* one could not account for a correct after an incorrect choice had once been made) YERKES found in one case that after 40, in another that after 250, experiences no mistakes in choosing were made. In a number of cases the subject turned from, before it reached, the partition which blocked the passage, thus showing the important part played by *vision* in directing the animal in the absence of smell, taste, and touch. All of these, however, together with muscular sensations, YERKES concludes *normally* play a part in the formation of labyrinth habits. These experiments therefore seem to show that upon the basis of the "constructs" which one sense alone, viz., vision, give the crab, a consistent selection of the correct path is possible; but this is explainable it seems, even if it is considered that only a recognition of each successive part of that path and consequently a discrimination between it and the incorrect is made, and yet that no *representation* or "*reconstruction*" of "aquarium" takes place, although of course this latter interpretation is not excluded.

A method of experimentation, however, which shows that in the formation of a habit, or in the learning of a motor reaction involving two sense fields, e. g., taste and vision, it is necessary to overcome an instinct or tropism in the opposite direction, such a method, we think, would at least give more cogent grounds for accepting the presence of *representation* than one not doing this, although even here conservatism in making this claim would be the safer course.

Some Characteristics of the Hermit Crab.

The genus *Eupagurus* is easily found in the shallower waters about Woods Hole and is represented by four species, *longicarpus*, *annulipes*, *acadianus*, *pollicaris*. *E. longicarpus* was selected for the present investigation on account of its convenient size ($\frac{3}{4}$ -1 $\frac{1}{2}$ inches in length) for aquarium purposes, and because of a manifestly greater brightness. Supplementary experiments show that *E. pollicaris*, e. g., learns with greater difficulty.

Members of the entire genus inhabit, under normal conditions, the shells of gastropods, by which the abdomen is completely protected, the cephalothorax alone protruding. This peculiar mode of life is correlated with a dextral asymmetry, which extends to almost all the organs of the entire body, and which shows a very nice adaptation. This favors the view that the asymmetry is a result of life in dextrally spiral shells, exemplifying at the same time degeneration.

The establishment of the fact that these Hermits learn is not surprising in view of the complexity and fineness of their physiological sense apparatus, which is essentially the same as that of all the Crustacea, so that it is very probable that any denial of this ability to any species of the group, even upon the basis of experiment, is due to incomplete or faulty methods of investigation.

Sense Organs.

The crab has only two general kinds of sense organs, viz., eyes and sense hairs, the latter of which are, however, differentiated as to their function. These hairs, which are found in all the extremities, are epithelial in nature, and are not penetrated by a nerve, but rather this latter spreads out underneath each epithelial group and gives to each cell a fibril. These epithelial sense cells lie in a support of "Matrixzellen,"¹ and according to variations in their structure and especially position are respectively gustatory, tactile, and auditory or "equilibra-

¹ VOM RATH, OTTO. *Zoologischer Anzeiger*, No. 386, 1892.

tory." The gustatory hairs, lie as two patches of "minute curiously flat organs" on the under surface of the outer filament of the antennules, the innermost appendages, which observation shows are kept moving constantly. There are no sense organs in the mouth.¹

At the basis of each antennule is a little sac formed by an infolding of the chitinous integument, communicating freely with the water, and containing little sand grains or otoliths. Here are present a second kind of sensory hairs, connected with the central nervous system by branches of the antennular nerve, and whose function is either that of audition or of equilibrium.² The third class of hairs are tactile in function, and are especially numerous on the antennae, i. e., the second pair of appendages, although there are some on the antennules, the other appendages, and the remaining integument.

The two eyes of the crab are compound or faceted and are seated on movable pedestals. They are covered by a transparent chitinous cuticle, forming a cornea; this is divided into facets, beneath each of which there is an ommatidium with two segments (a) an outer, which is vitreous and refractive, and an inner, a short retinula, which is sensitive, thus giving a structure analogous to rods and cones. These cones are surrounded and so separated from each other by a pigment; their apex is embraced by elongated cells in the midst of which is a fibril of the optic nerve. Each facet functions as a single eye and therefore like the vertebrate eye gives no sensitive continuum but, rather, "mosaic vision," i. e., various images in juxtaposition. The eye as a whole is supposed to give a vision of distinct objects and space relations.

The brain is formed from the first three pairs of embryonic ganglia, and is therefore a "syn-cerebrum"; it supplies the eyes, the antennules and the antennae with nerves. It is connected

¹ VOM RATH, OTTO. Zur Kenntniss der Hautsinnesorgane der Crustaceen, *Zoologischer Anzeiger*, 365, 1891.

² HENSEN (Studien über das Gehörorgan, *Zeitsch. f. wiss. Zool.*, Bd. 13, 1863) says they are auditory, while DELAGE, *Archiv. d. Zool. Expér.*, 1887, (2), T. 5, says they are for position and equilibrium. (Quoted by VOM RATH.)

by two oesophageal branches with the central nerve cord, which is represented principally by a single large thoracic ganglion or concrescence of ganglia. The thoracic portion of the nervous system is, however, symmetrical. The mandibles, or the third pair of appendages, crushing jaws, the right of which is larger, the maxillae and the maxillipeds all receive nerves. The nervous system is therefore in general so constructed that it would seem at least reasonable to expect that associations might be formed.

Experimental

The systematic experiments by which the association between the "constructs" of two sense fields, taste and vision, was established, and a "reconstruction" or reproduction subsequently shown possibly to take place, were preceded by various preparatory observations, some of which were made in the summer of 1902. For instance, it was then shown that the Hermit is remarkably *thigmotactic*, for when a shell inhabited by a crab is suspended at the distance of about twice the diameter of the shell from the floor of the aquarium, the animal is thereby made decidedly uncomfortable, protrudes nearly its entire body, feels about, and usually leaves its shell, especially if there is a vacant shell near by. Suspended at the height of from eight to ten inches the crab will remain in the shell until it dies. They are also somewhat rheotactic. New shells thrown into the aquarium are soon examined and accepted at what would sometimes seem to be a disadvantage. This constant "desire" for change, together with both a great natural rapacity and pugnacity, are indeed indications of a strenuous life even among Hermits.

Both that series of observations upon which special emphasis is placed in this paper, and that preliminary one which showed that the method adopted would probably lead to satisfactory results, were made with a very simple apparatus and in a very simple way. A number of crabs which had been kept in an ordinary laboratory glass jar aquarium about twenty inches in diameter, were made to go into a darkened portion of this that they might get their food, which consisted of a freshly

cleaned *Fundulus* held in place on a wire. The same portion of the aquarium was darkened each time just before feeding by setting down into the constantly running water a screen consisting of two thin boards fastened at right angles, leaving only an opening at each end of the vertical board wide enough for the crabs to go through one by one; around the outside of the aquarium from end to end of this portion set off by the screen was kept a piece of heavy brown paper to shut out the light coming from the other direction. The only light which could enter came therefore through the openings at each end. Sand was placed in the bottom of the aquarium, and all the conditions such as its position and that of the tap, with the exception of the putting in and taking out of the wooden screen, were kept constant during the entire series of experiments.

These were conducted in detail as follows: to establish, first, an association and, second, present an occasion for possible "reproduction" from the "after-effect" of one by the external stimulus of the other "construct."

Thirty-six crabs of the species *Eupagurus longicarpus* were placed in the aquarium on July 30th, and, first, allowed until August 6th to become accustomed to aquarium conditions; during this period they were simply fed each day with a fresh *Fundulus*, no screen being used; they seized their food most eagerly, oftentimes fighting and driving each other away from it. The death of six selected the thirty most fit individuals. The crabs were, furthermore, observed to remain in the *lightest* part of the aquarium practically all of the time, i. e., they were positively heliotropic. The positive heliotropism was confirmed by a number of control experiments with other lots and by that of Aug. 6th. The screen was inserted and all the crabs, 30 in number, placed behind it. In 10 minutes 28 had gone through the opening into the light and 27 of these were near the point of its maximum intensity.

Each day following this, the screen was inserted, a fish on a wire placed in the darkened portion, and the number of crabs going into the dark through *either one* of the entrances at the end within a given time, which was constantly shortened during

the series, counted. A crab going in and coming out again was counted as *in*, but in every case by far the greater number that had entered remained behind the screen as long as the food was there. Two stimuli to two different senses, taste and vision were thus simultaneously and contiguously presented; and if this led to an association between the two "constructs," "food" and "screen-darkness," it would necessitate the *overcoming* of the natural positive heliotropism manifested at the start, and by contrast on this background the association would stand out more prominently. After the crabs were fed each

EXPERIMENT I.

Lot 2, *Eupagurus longicarpus*.

	Total No.	No. entering.	Per cent.	Time.	Per cent. in 1'
1st day	30	3	10	15'	.66
2d day	30	14	46	20' ¹	2.3
3d day	30	15	50	75' ¹	.66
4th day	30	20	66+	15'	4.4
5th day	30	25 ²	83	5'	16.6
6th day	30	27	90	5'	18.
7th day	27 ³	26	96	3'	32.
8th day	29 ⁴	28	97	5'	19.+

¹ This long time was granted in order, if possible, that the crabs might ultimately find their way *in* as a result, perhaps, of merely wandering around in their evident endeavors to localize the source of the taste stimulus, which in every case caused considerable agitation. The *varying length of time* used throughout the series was a matter of *best adapting the means* to the end. Thus it was quite justifiable to shorten the time later to 3' if the majority of the crabs went through the openings in that time, although to do this would give manifestly more favorable results than to wait longer.

² On this 5th. as well as on each successive day up to the 9th. it was noticed that as soon as the screen was put in, and the fish was placed behind it, the crabs were much agitated and some started for the openings.

³ The three that did not go in on the previous day had been removed for the purpose of determining if possible if there was already a certain permanency of habit among the twenty-seven entering; the result was confirmatory. The three were then returned.

⁴ One had died.

day under these conditions, fish and screen were removed, and the latter was carefully washed with running sea water, as it was also each time just before using. After a few days of this treatment immediately upon the insertion of the screen the

crabs became most agitated, some hurrying and scurrying about, others making almost directly for one of the openings. A preference for the right-hand one seemed to exist and this may be connected with the right-handed asymmetry. No attempt however to investigate this matter systematically was made, and there were no "landmarks" in the aquarium, such as stones, etc., whereby a path could be learned. The preceding tabulated results show, (1) the total number each day, (2) the number going into the dark within (3) a certain time, when fed under the condition named, (4) the per cent. entering, and (5) for comparative purposes, the per cent. entering in one minute.

EXPERIMENT II.

Lot 2.

	Total number.	Number entering.	Per cent. entering.	Time.	Per cent. in 1'
9th day	28 { death } { of 1 }	24	86	5' ¹	17.2
10th day	28	22	79	5' ²	17.2
11th day	28	26	93	5'	18.6
12th day	28	25	89	5' ³	17.8
13th day	27	25	93	3' ⁴	31.
14th day	27	23 { in and } { remained }	85	3' ⁵	28.3
15th day	27	24	89	3'	29.6
16th day	27	22	82	3'	27.3
17th day	27	22	82	3'	37.3
18th day	27	22	82	3'	27.3

¹ At the end of the 5' the fish was put behind the screen in order that the association might not be broken up by the crabs entering and finding nothing there. When this was done all but one of the eight outside, four of which had gone in and come out again, entered within 2'. This was done each successive day.

² Then fed, and in 1' all but one had entered. This shows again the constant improvement, the learning taking place in a surprisingly short period.

³ In one minute after feeding all of the seven outside had entered.

⁴ After feeding all entered in 1½'.

⁵ After feeding all but one entered in 2'.

Accordingly, after the 8th. day, evidence having been thus secured that an association between the two "constructs," food and sense-darkness, had been established, its efficiency was

further tested by simply putting in the screen with no fish behind it, and the record of the crabs entering was taken in the same way as before. The results are tabulated above.

These results, if confirmed by control experiments, must, we think, be accepted as showing conclusively that the Hermit crab of the species *longicarpus*, firstly, forms an association between two sense-constructs, which, secondly, can be interpreted as showing that the crab, subsequently, when only one stimulus is presented, *reproduces* an image of the other. The same reaction, entering the dark, which previously demanded two stimuli, is later secured with only *one* stimulus; the other therefore must either be excited or reproduced. We may say perhaps that if, when only the screen is put in as in the second series, *only visual* perception or recognition takes place, then there is no reason why the crabs should not remain where they are, in the light, which is their natural preference. The screen, which they now recognize, has however through association come to mean for them other than something to be avoided; it means "food," and this meaning is present when the food is not. The difference between YERKES' experiments and these consists, therefore, in this, that YERKES' crabs "acquired the habit" of going by a correct path from a place disliked to a place liked; the Hermits on the other hand go from a place liked to a place naturally disliked, but "artificially" liked because of food either there or—may we say—"expected" to be there. This must mean that an associative element at first external, i. e., *physical*, but now no longer *that*, is, nevertheless, now present as *internal*, and its internal presence must be due to either an excitation or a reproduction by the other stimulus. If the latter, then the Hermit may be said to remember vaguely, i. e., to *reconstruct*.

These conclusions are strengthened by the following control experiments:

EXPERIMENT III.

Lot 4. Aug. 20th. Forty crabs in a similar aquarium; the same screen was used, carefully washed each time. The previous procedure was reversed here, by placing the crabs be-

hind the inserted screen first, and feeding in the light. From the data already obtained it would be expected that in this a greater per cent. of crabs would from the start make their exit than had in the first experiment made their entrance. This proved to be the case as the following record shows :

Number of crabs.	Exit.	Per cent.	Time.	Per cent. in 1'
40	34	85.	5'	17.
40	36	90.	3'	30.
40	35	87.5	5'	17.5
40	35	85.	5'	17.
40	34	85.	5'	17.

Comparison of this with Experiment I shows that not until the 5th. day was as high a ratio approximately obtained. In both cases of course the crabs are guided by taste; the two experiments together, therefore, serve to demonstrate the natural preference for the light, and the quicker results obtained when this works with than when against the feeding instinct.

EXPERIMENT IV.

Lot 3. This same preference was demonstrated by a second control experiment. Twenty-four crabs were placed in a large rectangular aquarium directly next to a window with a northeast exposure. Half of the aquarium was darkened by holding down with a stone a box with one end taken out. Sand was placed over the entire bottom.

Twenty observations failed to discover a single crab inside the "dark line" from edge to edge of the box. The crabs, therefore, seem to prefer the light to the darkness, at least in the aquarium.

EXPERIMENT V.

Lot 6. A third very similar control experiment was also confirmatory. Thirty crabs, the aquarium jar and screen exactly as in Experiment I were employed. The question might arise, would not the crabs possibly "learn" to go behind the screen when this was inserted even though no fish was there, the necessary feeding being done at other times. Should they do this the conclusions from Experiment I would be quite

worthless. The results were that they would not enter. Ten observations were made; in seven of these cases no crab (within 5') went further than to the edge of the entrance, which had in no experiment been counted as "in"; of the three other cases, within the period of 5 minutes, 5, 8 and 5, respectively entered, but there was no evidence of progress.

ADDITIONAL EXPERIMENTS.

Maze Experiment. Can the Hermit learn to go through a maze for its food? A simple maze was constructed of thin boards in such a way that it was necessary for the crabs, 16 being used, to enter at one end, go through to the other, enter the second passage, go back to the other end and enter the food compartment. The crabs were first given an opportunity to "become acquainted" with the maze by leaving it in the aquarium about two hours. The next day this was repeated with the result given in the first line of the table. The results are as follows:

Total No.	Successful.	Per cent "in."	Time.	Average in 1'
16	All	100	90'	.9
16	13	81	45'	1.8
16	16	81	55'	1.47
16	15	94	30'	3.13
16	8	50	30'	1.66
16	15	94	45'	2.09
16	14	88	30'	2.93
14 (2 died)	13	93	30'	3.1

This experiment was not conducted as carefully as it would be possible to make it; the crabs could not be watched all of the time, but only occasional observations and a record, as the above, at a stated time, made. The results showed, however, though perhaps not as clearly as might be desirable, that an improvement had taken place, and they have a value, as being in general confirmatory of the first experiment.

Conclusions.

The Hermit Crab, *Eupagurus longicarpus*, is capable of profiting by experience, in a rather short time, by associating

the "constructs" of two "sense fields," vision and taste. The existence of this association is proved by its effectiveness in subsequently bringing about, with only one stimulus presented, the same reaction against a natural positive heliotropism, as previously occurred with two stimuli present. The reaction here is therefore conditioned *internally*, as well as externally. The internal condition must be identical with either the excitation of, or with that and the reproduction from the "after-effect" of the second, the "taste-stimulus;" if there is only excitation then the internal event is only physiological; if there is also reproduction then it is psychical as well as physiological.

Both interpretations agree equally well with the data obtained, for the reason that even in the second case there must be a physiological basis for the psychical events if present, and consequently, the two being quite compatible as ultimately regular and uniform series of events, there is theoretically no certain objective criterion for the presence here of consciousness.

Practically there is, however, such an objective criterion which we make use of in our intercourse with other men, and if the above data are interpreted in as strict analogy to this as possible, it seems justified to consider that the Hermit Crab "reproduces" or, if one will, remembers vaguely.

The author, as a holder of one of its "research rooms" at Woods Hole wishes to acknowledge his indebtedness to the Carnegie Institution for the opportunities thus presented for the carrying on of this and other investigations.

Jan. 12, 1904.

EDITORIAL.

L' ENVOI.

The change recently announced and, by the appearance of this number, placed in process of realization means much to the writer. It means, among other things, the fulfillment of a cherished desire and the realization of hopes which led to the founding of the *Journal of Comparative Neurology* at a time when the prospect of either scientific or material support seemed very small. The small but growing band of investigators in this country were much better than their promise in supplying material and in supporting the enterprise from the start. In spite of the fact that the specific purpose of the venture was realized only in part, a fact partly to be accounted for by the long-continued incapacity of the writer, it is believed that the thirteen years of the existence of the *Journal* have not been entirely unfruitful.

It seems not inappropriate that the writer should avail himself of this occasion, apparently so full of promise for greater usefulness in the future, to express his personal gratitude for the unselfish toil which has been expended by the numerous collaborators on the staff during a period of nearly ten years, during which care on his part has been impossible and his own responsibility of the most perfunctory kind. To my brother, Professor C. JUDSON HERRICK, especially, who has carried the administrative and editorial responsibility, much of the time with little or no assistance, and on whom the financial burden has too largely fallen, the *Journal* owes its continued existence and the new lease of life to which we now look hopefully forward. Thanks are due also to the many others, both in this country and abroad, who have actively shared in the responsibilities

and have contributed from their original material, as well as to the numerous friends who at this emergency have contributed money to enable us to enlarge at once, pending the substantial increase in circulation which is already in progress.

At the time the earlier numbers were issued there was little of that *camaraderie* and acquaintance among the widely scattered workers in this, as in many other lines, which now is one of the pleasant and encouraging features of scientific work. With a growth of this fellowship we note with gratification the almost entire disappearance of the acrid or acrimonious criticism that disfigured early scientific literature in America. It is now possible to admit differences of opinion or to detect errors in the work of another without establishing forthwith a breach of cordial relations among the workers. C. L. HERRICK.

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Structure and function are correlative concepts; neither is complete without the other; as cause implies effect, so function implies structure. These are trite statements, yet it would seem that we can not be reminded too often that the understanding of life is dependent upon our ability to correlate structural and functional facts. It is chiefly in the interest of such correlation that *The Journal of Comparative Neurology and Psychology* is published. True, there is no more reason for considering the psychic process a function of the nervous system, than for calling the brain a function of consciousness; but, this aside, animal behavior and the functions of the sense organs and central nervous system are dependent upon neural structures, and it is these which most concern us. A survey of modern research literature shows clearly that those investigators have been eminently successful who have studied structure and function at the same time. To the physiology of the senses vastly more is contributed by those who know form as well as function, than by those who neglect anatomical conditions; in animal behavior, it is from the student who attends to anatomical and histological facts that a satisfactory account of the reactions of an organism is to be expected.

Throughout the organic realm a correlation of structure and function is demanded. It is our aim, in *The Journal of Comparative Neurology and Psychology*, to bring together anatomical, physiological and psychological facts in such a manner that their relations may appear. Thus, it is hoped, the specialists in structural work will be impressed by the importance of the functions of the organs which they study, while at the same time those whose chief concern is animal behavior will see more clearly that they cannot work to advantage unless they know *what* is functioning. If we are to understand life we must consider the organism not as a structural unit, nor yet as a sum of activities, but as a functioning structure.

R. M. YERKES.

THE MID-WINTER MEETINGS.

Though abstracts of the proceedings of most of the societies, which met during convocation week have already been published, it may be of interest to enumerate in a single list the more important papers read which bear upon our problems, as an aid to the annual invoice of scientific achievement which one naturally makes at this time of year.

At St. Louis the zoological section of the American Association and the Central Branch of the American Society of Zoologists held joint sessions at which the following papers of neurological interest were read:

Further Observations on the Breeding Habits and on the Functions of the Pearl Organs in Several Species of Erentognathi, by JACOB REIGHARD. The breeding habits of certain shiners and suckers were described and illustrated by instantaneous photographs.

Phototaxis in Ranatra, by S. J. HOLMES. *Ranatra* is positively phototactic and a great variety of reactions can be produced at will with mechanical precision.

The Correlation of Brain Weight with Other Characters, by RAYMOND PEARL. A statistical review of the data for the human brain.

The Morphology of the Vertebrate Head from the View-point of the Functional Divisions of the Nervous System, by J. B. JOHNSTON. This paper will appear in full in this *Journal* in the course of the current year.

The Brain and Nerve Cord of Placobdella pediculata, by E. E. HEMINGWAY. Wax models of the nervous system of this new leech were presented. The results in general confirm those of WHITMAN for *Clepsine*.

The Mechanism of Feeding and Breathing in the Lamprey, by JEAN DAWSON. The anatomical work was controlled by observations on the living animals which add to our knowledge of the habits of the species, notably the fact that the lamprey feeds on the soft tissues as well as the blood of its host.

Some Reactions of Mnemiopsis leidyi, by G. W. HUNTER. This paper will be published in this *Journal*.

A Theory of the Histogenesis, Constitution and Physiological State of Peripheral Nerve, by PORTER E. SARGENT. To be printed shortly in full in this *Journal*.

The Association of American Anatomists met in Philadelphia. There were five neurological papers, aside from the memoir by Dr. WILSON which appears in our present issue.

On the Origin and Destination of Fibers of the Occipito-temporo-pontine Bundle (Türk's Bundle, Meynert), by E. LINDON MELLUS. In a circumscribed experimental lesion of the cortex of the temporal lobe in the monkey, involving the first and second temporal convolutions projection fibers degenerated, passing by way of the sub-lenticular segment of the internal capsule to the pes pedunculi, where they occupy the external fifth (occipito-temporo-Brückenbahn, FLECHSIG; sensory tract, CHARCOT and others). To reach the pes these fibers break through the inferior portion of the lenticular nucleus in small bundles, pass around the external geniculate body just above the point of exit of the optic tract and enter the pes external to those fibers which form the posterior extremity of the internal capsule as it passes between the thalamus and the lenticular nucleus. Instead of turning downward toward the pons, like the capsular fibers, they pursue a course obliquely backward and slightly downward and, after a very short course in the pes, disappear, apparently passing to the anterior quadrigeminal body.

The Brains of Three Brothers, by EDW. ANTHONY SPITZKA. Opportunities for demonstrating the influence of heredity in the configuration of the human brain are exceedingly rare; adult material of this kind has only once before been described and by the same writer before this Association three years ago in the case of the brains of the two distinguished physicians SEGUIN, father and son. It may be remembered that in the SEGUIN brains there were found some notable resemblances which could be attributed to hereditary transmission. The writer again had the good fortune to test the question of encephalic morphological transmission in the brains of three brothers recently executed together in New York State. In the search for positive evidences of hereditary resemblance, only such parts of the cerebrum as are subject to great range of variation in different brains could be depended upon to support the proposition; it was found, in fact, that peculiarities of anatomical configuration of this class, uncommon enough in the general run of brains as they come to the

hands of anatomists, were similarly reproduced in the three brains. Illustrations were given.

The Bimeric Distribution of the Spinal Nerves in Elasmobranchii and Urodela, by CHARLES R. BARDEEN. In those vertebrates in which a definite metameric segmentation is maintained in the body wall, both the cutaneous and the motor nerves of each segment reach their distribution through the myoseptum and supply structures both cephalad and caudad to their septum. Occasionally a single motor nerve fiber may be seen dividing and sending one branch to the myotom anterior to the septum and the other to the myotom posterior. Attention is called to the difficulty of reconciling these facts with a strict adherence to an extreme form of the neuro-muscular theory such as is maintained by some morphologists.

A Description of the Gross Anatomy of the Adult Human Brain, by BERN BUDD GALLAUDET. The description was confined to the thalamus and was based on forty adult brains.

On the program of the Eastern Branch of the American Society of Zoologists, meeting at Philadelphia, the following titles, among others, were announced:

The Physiology of the Lateral Line Organs in Fishes, by G. H. PARKER. To appear in abstract in this *Journal* and in full in the *Bulletin of the U. S. Fish Commission*.

A Pair of Giant Nerve Cells of the Squid, by LEONARD W. WILLIAMS.

The Nervous System of Lamellibranchs, by GILMAN A. DREW.

The Origin and Function of the Medullary Sheaths of Nerve Fibers, by PORTER E. SARGENT. To appear in full in this *Journal*.

The Relation of the Size of Nerve Elements and Their Constituent Parts to Structural and Functional Conditions, by PORTER E. SARGENT.

At the Philadelphia meeting of the American Physiological Society the following papers, of special interest to neurologists, were read:

The Survival of Irritability in Mammalian Nerves after Removal from the Body, by W. D. CUTTER and P. K. GILMAN. Making use of the fact noted by other observers that the mammalian nerve retains its irritability for some time after removal from the body, the authors attempted to determine the duration of this survival, the variations in irritability during the period of survival, and, lastly, the effect of prolonged anæsthesia upon the phenomenon. Irritability was determined by measuring the action current of the nerve when

stimulated by a series of induction shocks. The experiments were made upon dogs, and the sciatics of both legs were taken for observation. One sciatic was removed as soon as the animal was anæsthetized sufficiently for the operation. The nerve was placed at once in the moist chamber, and its action current was determined at intervals of half an hour, as long as a response could be obtained to stimulation. With the values of these action currents as ordinates, a curve was constructed, showing the duration and variations of irritability in the "unanæsthetized nerve" during the period of observation. The other sciatic was left in the animal for a period of four to six hours, and during this time the animal was kept completely anæsthetized by morphia and ether. At the end of this period, there was a considerable fall in rectal temperature (30° – 31° C.). The anæsthetized nerve was then removed, and galvanometric observations were made similar to those just described. The results obtained show that the nerve removed from the anæsthetized (and cooled) animal survives for a longer period than that taken from the animal at the beginning of the period of anæsthesia, the difference in time of survival being as much as four or five hours. A more marked difference, however, is that the "anæsthetized" nerve exhibits throughout a much greater irritability. The curves obtained were irregular; but that for the "unanæsthetized" nerve shows a small increase in irritability occurring shortly after the excision, and soon followed by a steady decline to zero; while that for the "anæsthetized" nerve exhibits, as its most marked feature, a large and sudden increase in irritability coming on some hours after the excision, and followed by a more rapid fall to zero.

The Condition of the Vaso-constrictor Neurones in "Shock," by W. T. PORTER and W. C. QUINBY. The normal fall of blood-pressure produced by stimuli of uniform intensity applied to the central end of the depressor nerve was measured in the rabbit and the cat. In the same animals the shock was then brought on, and the measurements repeated. The experiments make clear (1) that the normal percentage fall in blood-pressure may be obtained by stimulating the depressor nerve during shock; (2) if during shock the blood-pressure be raised to normal values by the injection of suprarenal extract or normal saline solution, and the depressor nerve be stimulated while the pressure is still high, the absolute fall in blood-pressure may be as great as it was in the same animal before shock began. Exhaustion of the vaso-constrictor neurones cannot therefore be the essential cause of the symptoms termed shock.

Demonstration of Rabbit's Nerves, Showing the Effect of Ligation

upon Vital Staining, by S. J. MELTZER. A single ligation of a nerve has no influence upon the staining of the nerve on either side of the ligature. When, however, two ligatures are applied, the section of the nerve between the ligatures remains free of color, while both ends are stained. This is the case, even if the section between the ligatures comprises nearly the entire length of the nerve.

The Effect of a Subcutaneous Injection of Adrenalin on the Eyes of Cats whose Sympathetic Nerve is Cut, or whose Superior Cervical Ganglion is Removed, by S. J. MELTZER. When the sympathetic is cut, a subcutaneous injection of adrenalin causes a retraction of the nictitant membrane, and no change is seen in the size of the pupil or the width of the palpebral fissure. When, however, the superior cervical ganglion is removed, an injection causes a strong dilatation of the pupil, a considerable widening of the palpebral fissure, and a retraction of the nictitant membrane.

The Delineation of the Motor Cortex in the Dog, by H. CUSHING.

Demonstration of Expressive Motions in a Decerebrate animal, by R. S. WOODWORTH.

At the meeting of the American Philosophical Association at Princeton the paper, "An Establishment of Association in Hermit Crabs," by EDWARD G. SPAULDING, which we publish herewith, was read. There was one paper on comparative psychology read at the meeting of the American Psychological Association at St. Louis.

A Preliminary Paper on the Psychology of the English Sparrow, by JAMES P. PORTER. Experiments were made with the food box, with SMALL's complex maze and in other ways to determine the method of approaching the food, to investigate the so-called senses of number and of direction and the color preferences.

A paper was read before the section of physics of the American Association at St. Louis, which is of some interest to physiologists, especially when taken in connection with the physiological experiments of NAGEL on the rate of diffusion of odors and savors in water.

The Rate of Propagation of Smell, by JOHN ZELENY. Attention is drawn to the extreme slowness of diffusion of odors in air tubes where convection currents are avoided. The time required for the diffusion of odors is roughly proportioned to the square of the distance.

LITERARY NOTICES.

Animal Education.¹

Under this title Dr. WATSON has published the results of a study of the white rat made for the purpose of correlating the psychical development with the growth of the nervous system. The work is naturally divided into three parts: (1) an experimental study of the psychical development; (2) an histological study of the central nervous system, for the purpose of tracing the development of medullation, and (3) a correlation of the psychical facts with the neurological facts.

Part I. The ability of the white rats at different ages to form simple associations was tested by various forms of the labyrinth method. The obtaining of food was employed as a motive. Usually the food was placed in a box and the animals were given a chance to get it by finding a hidden opening into the box, by opening a spring door, or by wending their way through a labyrinth. The observer watched the behavior of the animals, and recorded the time required for the accomplishment of a given act. The results of this psychological study include certain interesting points of difference between young and mature rats which cannot be better stated than in the words of the author:

1. No form of problem which the adult rat is capable of solving presents insurmountable difficulties to the rat of twenty-three days of age.

2. a) The time of first success in solving problems conditioned chiefly upon physical activity is shorter for young rats than for adults.

b) For the second solution of such a problem, adult rats do not require a longer time than young rats.

c) Problems not so conditioned upon physical activity are solved, even the first time, more quickly by adult than by young rats.

3. a) Young rats make many more useless movements than adult.

¹ WATSON, JOHN B. *Animal Education: An experimental study on the psychical development of the white rat, correlated with the growth of its nervous system.* Chicago, *The University of Chicago Press*, 1903, 122 pp., 22 Figs., 3 Plates.

b) After once associating the various parts of a problem, adult rats make only the movements necessary to attain the desired end, while young rats—owing to their superabundant physical activity and lack of muscular control—continue to make useless movements long after adult rats have discarded them entirely.

c) There is a gradation in the number of useless movements made by rats at different ages. At thirty-five days of age, when physical activity appears to have reached its highest stage, the percentage of useless movements is largest. As the rats grow older this superabundant activity disappears, and in its place comes direction of activity.

Concerning the stages of memory the author writes :

1. Until the rat has reached the age of twelve days, life to it is simply a matter of pure instinct. Certain movements are made, but these movements are dependent upon the ready-made adjustments of neural and motor elements with which the rat begins life ; intelligence plays little or no part.

2. At twelve days of age memory is present in a simple form.

3. From the twelfth to the twenty third day there is a gradual but rapid increase in the complexity of the memory processes until at the latter age psychical maturity is reached. Development after this age is analogous to the development that takes place in a child of ten years as he gradually becomes more and more mature.

Parts II and III. Having investigated the capacity of rats to learn simple associations, at different stages of development, the author proceeded to make a careful histological study of the changes which occur in the nervous system from birth to maturity in order that he might be able to correlate the psychical and neural conditions and definitely determine whether associations are dependent upon the medullation of nerve fibers. As a result of this work Dr. WATSON concludes : (1) that the “medullated fibers in the cortex of the rat are not a *conditio sine qua non* of the rat's forming and retaining definite associations, and (2) that the complexity of the psychical life increases much more rapidly than does the medullation process in the cortex, psychical maturity being reached when approximately only one-fifth of the total number of fibers in the cortex are medullated.”

Instead of speculating about the general significance of medullation the author very wisely confines himself to the discussion of his own particular facts. The experimental work is clear cut and decisive, and if one sometimes feels that fewer words might have sufficed and and space been saved by the condensation of results into tables, the excellent summaries more than compensate for the lengthiness of the descriptions. Dr. WATSON has done a valuable piece of work in a field which has been open thus far for the theorizing of neurologists and psychologists.

ROBERT YERKES.

Metaphysics in Comparative Psychology.¹

The first of these articles is a defence of the comparative method in psychology in general, but more particularly when based upon an identity theory of the relation of brain and consciousness. He criticizes that school of comparative psychologists which attempts to reduce all forms of animal reactions to the type of mechanical tropisms, asserting that this tendency toward a mechanical interpretation is the direct product of false metaphysical assumption—that of psychophysical parallelism. Instead of this, the author upholds a theory of identity which makes it possible for him to put “Seele” in parenthesis after “Gehirn.”

The arguments with which he attacks the parallelistic doctrine are familiar enough and will perhaps pass muster; at least they are the usual arguments wielded in current controversy. On a parallelistic hypothesis, when the one series is complex, the other should be complex, and *vice versa*: but this is not the case. The psychical sequence, which, on the parallelistic theory, ought to form a continuous whole is arbitrarily broken without any assignable cause, or the psychological causes which are assigned prove, on closer inspection, to be inadequate. Both of these arguments, in the opinion of the reviewer, can be met by the parallelist. But let it pass. More important for criticism are the positive arguments brought forward in support of the identity doctrine.

The author points out that there are important brain centers which are inaccessible to present physiological experimentation and which seem to bear no direct relation to our ordinary consciousness. Consciousness corresponds to a comparatively limited phase of cerebral activity. Indirectly, however, the content of consciousness is influenced to a high degree by the activities of these centers. It is not astonishing, therefore, that the psychophysical law does not hold. (He does not say so, but presumably this is because of the inhibitory effect of competing stimuli originating in these centers.)

Instead of regarding this as evidence simply of an unsuspected complexity in the conditions of that shifting area of tension which con-

¹A. FOREL. Die Berechtigung der vergleichenden Psychologie und ihre Objekte. *Journal für Psychologie und Neurologie*, Band I, Heft 1 und 2, pp. 3-10 (1902); Beispiele phylogenetischer Wirkungen und Rückwirkungen bei den Instinkten und dem Körperbau der Ameisen als Belege für die Evolutionslehre und die psychophysiologische Identitätslehre. *Ibid.*, Band I, Heft 3, pp. 99-110 (1902); Ants and Some Other Insects, *Monist*, Vol. XIV, No. 1. Oct. 1903; Jan. 1904. Tr. by W. M. WHEELER.

stitutes consciousness he, however, regards it rather as evidence of an infra-consciousness corresponding to, or rather he would say, constituting these inaccessible cerebral activities. What more natural than to assume, he says, that every cerebral activity has its introspective or inner counterpart, if not in our ordinary upper consciousness, then in this lower consciousness. Here is the key to the author's point of view and to his identity theory, and the reader who has already threshed out the problems here involved will doubtless turn to more instructive reading. There is no fallacy which to a greater extent vitiates the arguments ordinarily brought forward in support of this theory than the doctrine of subconscious mental states.

Under cover of this concept of a lower consciousness, the author finds it possible to attribute, not only consciousness but in some cases a high degree of consciousness to the lowest types of animals, e. g., to the *Arcellae* described by ENGELMANN. He finds evidences of memory, perception, association, feeling, choice in ants and bees. He says that the domestication of certain insects proves their plasticity, and finds evidence of this trait even in worms and echinoderms. Obviously, the significance of such statements must be interpreted in terms of his theory of unconscious mind.

His second article treats more in detail of the habits of various species of South American ants—which, again, he makes corroboratory of his identity doctrine. That there is truth in some form of the identity theory is extremely probable. One will perhaps agree with the author when he says that logically there is no more direct connection between my individual psychology and your individual psychology than there is between my individual psychology and the physiology of my brain. Hence actions, gestures, movements, attitudes, are as significant for psychology as sense-impressions. Human psychology is, and must be, comparative psychology.

But when he says that environment influences brain (soul) through the sensory nerves, and brain (soul) influences the muscles, glands, etc. (and thus the environment) through the motor nerves, one begins to feel that the meanings of words are becoming confused. And this feeling is increased when he adds that the soul is the brain-activity reflected in consciousness. One suspects that the concept of a lower consciousness is simply a screen behind which the author may slip unnoticed from one meaning of a word to the other according to the exigencies of the argument.

But quite apart from this, it must be remembered that the brain-activity, which the author identifies with the soul-activity, cannot be

isolated from the activities of the whole organism. It is probably true that the brain activity and the so-called mental activity are ultimately one, but it certainly is neither good biology nor good psychology to attempt to identify the latter with the former in any sense which opposes these to non-nervous organic or to the extra-organic processes. The author unquestionably has hold here of an important truth, but it is a truth still in solution—still fluid, not yet precipitated in a form that is quite consistent. In truth, this is just the desideratum in the current controversy as to the nature of the relation existing between the physical and the psychical—a statement of the law of the conditions of consciousness which will not violate the principle of continuity in nature.

The article in the *Monist* on "Ants and Some Other Insects," translated from the German by Professor WILLIAM MORTON WHEELER, is an "inquiry into the psychic powers of these animals with an appendix on the peculiarities of their olfactory sense." This is an account of some very interesting experiments upon ants and bees, prefaced, as in the case of the other two papers, by a metaphysical introduction. As in the former articles, he finds evidence of the possession in these insects of memory, association, will, etc. The experiments are certainly instructive even though one is inclined to regard the interpretation of results as infected detrimentally by the metaphysical standpoint. The standpoint here again, while suggestive, seems untenable. One is pleased with the statement that "we can therefore compare attention to a functional *macula lutea* wandering in the brain, or with a wandering maximal intensity of neurocymic activity" (p. 36). But we are astonished then to be told that "if this assumption is correct . . . we are not further concerned with consciousness. It does not at all exist as such, but only through the brain-activity of which it is the inner reflex. . . . Consciousness is only an abstract concept, which loses all its substance with the falling away of 'conscious' brain-activity" (37). In other words, the author adopts the identity theory and wholly rejects the parallelism. And the criticism, in a word, is this, that he has thus cast aside the very element that makes the identity intelligible.

H. HEATH BAWDEN.

Claparède on Animal Consciousness.¹

The present article is in large measure a revision, or restatement, of the author's contribution to the subject in the *Revue Philosophi-*

¹ EDOUARD CLAPARÈDE. The Consciousness of Animals. *The International Quarterly*, Vol. VIII, pp. 296-315. Dec., 1903. Translated by WILLIAM HARPER DAVIS, Columbia University.

que,¹ worked over for the benefit of English readers. After a brief glance at the history of the problem, the present reaction of biologists against the anthropomorphic tendencies of the Darwinian period, and the attempts of LOEB, BETHE and others, to reduce the activities of lower organisms to simple physico-chemical tropisms are discussed in detail.* The question is pointedly asked, why are tropisms necessarily unconscious? In all probability they are a great deal more complex than they are assumed to be by these investigators, and in any case it is difficult to discover any difference in kind between tropisms, reflexes and voluntary acts.

Any such objective tests of consciousness as LOEB's "associative memory", or WATKINS' "spontaneity" are quite beside the mark, for they overlook the fact that consciousness is and can be only subjective. The only legitimate point of view for approaching the problem is that of psycho-physical parallelism, the principle which assumes that for every change in consciousness there is a parallel and corresponding change in the nervous system. Just what the relation is that subsists between the two is as yet undetermined, but at any rate we must look upon them as two distinct series, and therefore it does not make a particle of difference, so far as the external series of acts is concerned, whether a biological process is conscious or not. If biologists would realize this fact, and cease trying to bring in the mind as a biological factor which exerts an influence on the body, much confusion would be avoided. So far as physical acts are concerned, consciousness is an epiphenomenon.

BETHE and his associates have gone to the other extreme in their efforts to get a perfectly objective nomenclature for all reactions to stimuli. They deny the possibility of psychic states in animals, or at least the possibility of gaining such knowledge of them as will furnish material for science, and hence they demand the suppression of comparative psychology. But any such argument would apply to human psychology as well. Comparative psychology is here and cannot be suppressed. From the standpoint of psycho-physical parallelism there are two parallel methods of studying life activity: (1) the *ascending*, or physiological, beginning with the lowest organisms and going on to the highest, explaining everything on purely physico-chemical principles; (2) the *descending*, or psychological, going down from man, and reasoning by analogy as to the mental life of animals. Both of these

¹ EDOUARD CLAPARÈDE. Les animaux sont-ils conscients? *Revue Philosophique*, tome LI, pp. 481-498. 1901.

lines of investigation are necessary, and they should not conflict, but should supplement each other. But as to the problem of the appearance of consciousness in the world, we must continue to say: *Ignorabimus*.

J. CARLETON BELL.

The Measurement of Mental Traits.¹

Those interested in the scientific study of education will welcome this book as a contribution to its methods. Professor THORNDIKE, following the line of GALTON'S famous researches, undertakes to bring together in a brief space such of the reliable statistical methods as have already proved fruitful or promise fruitful results in the study of mental traits, especially of school children and college students. Perhaps the greatest value of the book, as the author himself foresees, will be to bring home to educators, more forcibly than heretofore, the untrustworthy character of the current generalizations on education, and to create a demand for inductive statistical study of the facts, such as those being carried on by Professor CATTELL, himself, and others, in our own country.

The implied assumption underlying the whole treatment in this book is that of the possibility of mental measurement. This does not mean an attempt to measure that timeless and spaceless, that incommensurable, abstraction that often goes by the name of the "mental" in discussions of the mind-matter problem. It means measurement of the behavior of an organism in terms of those reactions which have come to be called mental because of their relations to the so-called higher values in life—but essentially identical in principle with physical or medical measurements. It is in this sense, apparently, that the author seeks "units of mental measurement" (p. 169), comparable to the inch, the ounce, the ohm, the ampere, the calorie, etc., in physical science. The difficulty is a practical one only. There is no inherent theoretical reason why such a unit may not be found and used. The variability of mental traits renders measurements approximate only. But this is true ultimately of all measurements; they are all anthropic at first. And approximate accuracy is better than the vagaries of current theory, while "the greater the number of measurements, the closer the approximation will be."

If education is to become a science, the physical and mental meas-

¹ E. L. THORNDIKE, *Educational Psychology* (Library of Psychology and Scientific Methods, edited by J. McKEEN CATTELL). *New York. Lemcke and Büchner, 1903.*

urements upon which its conclusions are based must be exact. We have a body of general but inexact knowledge about instincts, habits, memory, attention, interest, reasoning. We have descriptions of these in the literature of child-study and methods of teaching. We have a great many general ideas about the influence of inheritance, environment and general mental development. But we have little or no accurate knowledge on these points.

Not much value is attributed to those "Broader Studies of Human Nature" (Chapter XIV), carried on mainly by the *questionnaire* method, which have emanated from the Clark University school of child-study. The possibility of a scientific study of the loves and hates, fears, interests, ideals, habits, motives and opinions, influence of books, games, toys, etc., is not denied but doubt is cast upon the accuracy of the methods used and the reliability and importance of the generalizations. "Information about 1000 people with respect to one trait is of far less importance than information about 100 traits in each of 10 individuals" (p. 161).

After discussing the possibility of mental measurement (Chapter II), the author takes up the problem of "The Distribution of Mental Traits" (Chapter III). Is there any law of distribution of mental traits in groups of individuals? As between the sexes? As between groups having different inheritance or different training? Can we treat courage, honesty, ambition, eminence, as we can treat color of eyes or hair or weight, statistically? The reply is in the affirmative. But we must beware of imagining "that nature has provided distinct classes corresponding to our distinct words, e. g., normal and abnormal, ordinary and exceptional," genius and idiot, precocious and retarded, bright and dull, etc. (p. 22).

In Chapter IV we have a discussion of "The Relationships Between Mental Traits." Alteration of one function involves others. Educational problems involving this principle are the question of the disciplinary value of studies, arrangement of groups of electives, systems of grading and promotion, tests of mental growth and condition. The relationships are often very different from what the educational literature would have us believe. "The striking thing is the comparative independence of different mental functions even where to the abstract psychological thinker they have seemed nearly identical" (p. 28). The mind is a dynamic, organic, functional whole; not a mechanical whole. It is like the nervous system—a hierarchy of relatively independent activities, "a collection of protoplasmic bands." We have memories not memory, specific habits of attention not a general faculty

of attention ; reason is a name for a host of particular capacities. "It follows that an individual's status in any one function need not be symptomatic of his status in others." Hence the fallacy of college entrance examinations as accurate measure of mental traits, and the folly of using any one study, such as arithmetic, as the basis of promotion.

In Chapters V and VI Professor THORNDIKE discusses the important questions of "Original and Acquired Traits," and "The Inheritance of Mental Traits." "What ancestry does is to reduce the variability of the offspring and determine the point about which they do vary" (p. 48). There is no theoretical reason why we may not measure the variation and inheritance which determines family resemblance. The author starts, of course, from the work of GALTON, and discusses the small amount of really scientific work which has been done in this field. He does not mention the recent work on MENDEL'S law, which certainly has a bearing. Nor is there any reference to the doctrine of organic selection of OSBORN, MORGAN and BALDWIN as offering a possibility of mediation between the extreme views of the transmissionists and the non-transmissionists.

Chapter VII is on "The Influence of the Environment." Here, again, it is perfectly possible to measure the influence of change in climate, food, school-training, friendship, sermon, occupation, etc. But we must avoid the fallacy here "of attributing to training facts which are really due to original nature or selection." The author would substitute for such vague and indefinite terms as culture, discipline, training, practice, imitation, the conceptions of "(1) Furnishing or withholding conditions for the brain's growth and actions ; (2) Furnishing or withholding adequate stimuli to arouse the action of which the brain is by original nature or previous action capable ; (3) Reinforcing some and eliminating others of those activities in consequence of the general law of selection in mental life" (p. 77).

One of the most valuable Chapters in the book is Chapter VIII on "The Influence of Special Forms of Training Upon General Abilities." "Does the study of Latin or of mathematics improve one's general reasoning powers? Does laboratory work in science train the power of observation for all sorts of facts?" In other words, "How far does the training of any mental function improve other mental functions?" (p. 80). There is no doubt that there is some influence. The question is, "To what extent and how" does this take place? "Learning to do one thing well has much less influence upon one's other abilities' than educational theorists would have us think. The general conclusion from his own experiments is "that a change in one function alters any other

only in so far as the two functions have as factors identical elements" (p. 80). "Improvement in any single mental function need not improve the ability in functions commonly called by the same name. It may injure it" (p. 91). There is no "general ability." Upon this the author repeatedly insists. The present reviewer thinks that Professor THORNDIKE carries his idea of the independence of the mental functions to a point which threatens the unity of the mental life. One wonders how a mind such as the author describes ever could perform such a synthesis as that involved, for example, in writing book on Educational Psychology. He says that "the mind must be regarded not as a functional unit nor even as a collection of a few general faculties which work irrespective of particular material, but rather as a multitude of functions, each of which is related closely to only a few of its fellows" (p. 29). "The mind is really but the sum total of an individual's feelings and acts" (p. 30). "This view is in harmony with what we know about the structure and mode of action of the nervous system. The nervous system is a multitude of connections between particular happenings in the sense organs and other particular events in the muscles" (p. 30).

These unguarded statements surely must be accounted for as the result of a violent recoil from the extremes to which the "abstract psychological thinker" has carried the faculty psychology. It cannot be that Professor THORNDIKE means to deny the important structural and functional unities found in the nervous system and in conscious process.

Chapter X treats of "Changes in Mental Traits with Age," and Chapter XI of "Sex Differences in Mental Traits." No mention is made of Professor HELEN BRADFORD THOMPSON'S recent work on "Psychological Norms in Men and Women." Chapter XII is on "Exceptional Children," especially defective children. A brief concluding chapter puts the "Problem of Education as a Science." An Appendix contains an "Index of Tests," of "Common Measures," and "Suggestions for Investigations in Educational Science."

The author is rather cavalier in his treatment of educational theory. But most of his readers will probably forgive him for that. As before remarked, the book is chiefly valuable as setting the task and suggesting the methods of a scientific study of education. It can scarcely be said that it adds much of positive value in the way of conclusions from data already studied. There are very few of the generalizations contained in this book which it would be safe to adopt without further vindication of their truth. But it certainly will stimulate more

exact methods of study of mental traits in relation to education, and this is more than justification for its appearance at this time.

H. HEATH BAWDEN.

Are Sounds, Made in the Air, Audible in the Water?

In their works on the sense of hearing in fishes and crustacea, KREIDL, BEER and PARKER have laid more or less emphasis on the reflection of sound waves in the air from the surface of the water. PARKER says (basing his statement to some extent upon experiment), "the plane separating air and water is, under ordinary circumstances, an almost impenetrable one for most sounds, whether they are generated on one side or the other of it, and many of the negative results obtained by previous investigators on the sense of hearing in fishes may have been due not so much to the absence of hearing in the animals experimented upon as to their inaccessibility to the sound, or at least to sound of an intensity sufficient to stimulate."

Interesting experimental evidence on this question is furnished by Dr. V. DUCCESCHI,¹ of Naples, in a recent number of the *Rivista d'Italia*. Struck by the fact that some boys, diving along the shore, were able to repeat, on emerging from the water, the words called to them by their comrades while they were still beneath the surface, he secured the services of an expert diver, provided himself with a boat and some simple apparatus, and set out to test the matter experimentally. Trials were made at various depths up to seven meters. The length of time that the diver remained under water was about 10 seconds. At 5 meters the diver could hear distinctly, and repeat on coming to the surface, every word called to him from the boat. At 6 meters he could distinguish between the sounds of two glass bells of different sizes, a whistle and a small trumpet, all sounded in the air, could tell how many times each one was sounded, and in what order. At 7 meters the diver was able to distinguish the sounds with much less certainty, and sometimes not at all. The high tones were found to be much more difficult to distinguish than the low.

The same set of experiments was tried when the water was somewhat rough, with the result that the sounds were perceived with slightly less accuracy. It is true that in all these experiments the possibility of the sound being communicated through the boat to the water is not excluded. Moreover DUCCESCHI thinks it may be a question whether

¹ V. DUCCESCHI. Gli animali aquatici possiedono il senso dell'udito? *Rivista d'Italia*, Anno VI, pp. 958-966, Dec., 1903.

the sounds were perceived through the ears or through the bones of the head, as stopping the ears with vaseline did not seem to affect the perception.

J. CARLETON BELL.

Edinger and Wallenberg's Bericht.¹

We heartily welcome the appearance of this *Bericht* printed as a *Separat* of convenient form. Six hundred and twenty-eight titles are noticed in two hundred and seventy-two small pages. About one-tenth of the work is devoted to vertebrates below the mammals. The greater part of the whole work is now done by WALLENBERG.

J. B. J.

Substitution of Function after Nerve Anastomosis.

Some interesting side lights on the plasticity of the associational paths within the human cerebral cortex are thrown by a recent surgical case² in which, after traumatic destruction of the facialis root and resultant paralysis, the central end of the spinal accessory nerve was sutured on to the peripheral facialis and a successful union effected. There resulted total permanent paralysis of the trapezius and sternomastoid muscles and almost perfect restoration of facial symmetry both at rest and (less perfectly) in the facial movements.

The account of the case is illustrated by numerous photographs taken before the operation for anastomosis and at various stages during the restoration of the function. The case brings into unusually sharp prominence the problem involved in the resultant alterations in the central associational paths and suggests a plasticity of cortical paths quite at variance with some of the current theories.

C. J. H.

The Cerebral Commissures Again.³

Professor G. ELLIOT SMITH takes as his text a remarkable aberrant commissure found only in the forebrain of *Sphenodon* and the true lizards and subjects the commissures of the hippocampal region of amniote vertebrates to a critical comparative examination. This aberrant commissure he finds to be "a bundle of fibers derived from

¹ Bericht über die Leistungen auf dem Gebiete der Anatomie des Centralnervensystems in den Jahren 1901 und 1902. Von Prof. Dr. L. EDINGER und Dr. A. WALLENBERG. *Leipzig, Verlag von S. Hirzel*, 1903.

² CUSHING, HARVEY. The Surgical Treatment of Facial Paralysis by Nerve Anastomosis. *Annals of Surgery*, XXXVII, 5, May, 1903.

³ SMITH, G. ELLIOT. On the Morphology of the Cerebral Commissures in the Vertebrata, with special Reference to an Aberrant Commissure found in the Forebrain of Certain Reptiles. *Trans. Linn. Soc. London*, 2 Ser., VIII, 12, July, 1903.

the caudal portion of the hippocampus, and therefore homologous (in part) with the psalterium of the Mammalia. But its behavior presents a marked contrast to that of the Mammalia: for, instead of pursuing an extensive forward course to cross over in the lamina terminalis, it avails itself of the primitive direct connection between the caudal lip of the cerebral hemisphere and the optic thalamus, and in this way reaches the roof of the third ventricle directly." Examination of certain amphibian brains leads the author to conjecture that here the aberrant commissure is represented, not in the dorsal commissure of the lamina terminalis, but in the superior commissure of OSBORN! Apparently there is here an interesting problem in cerebral morphology which remains to be worked out in the Ichthyopsida. C. J. H.

The Homologies of the Cerebellar Fissures.

Professor O. CHARNOCK BRADLEY¹ attacks this intricate problem using a combination of the methods of comparative embryology and comparative anatomy, building upon the foundations laid by STROUD and KÜITHAN. He recognizes that we must not begin by seeking homologues of the human fissures in lower animals; but that, beginning with the smoothest and least complicated cerebellum, the fissural pattern should be worked out in the ascending series of mammalian complexity.

The paper opens with a description of the developmental stages of the cerebellar surface in the rabbit, after which comparison is made with other simple adult cerebella; viz., the hare, shrew, hedgehog, mole, rat, water-vole, bat and squirrel. The second part of the paper includes a similar description of the development of the pig, with comparison with the marten, badger, dog, fox, cat, goat, sheep, cow, horse and donkey. This is followed by a provisional application of the results to the subdivision of the human cerebellum in the light of the comparisons made. The paper is illustrated by numerous outline figures.

In a later paper Professor G. ELLIOT SMITH² controverts the author's position regarding the relations of the flocculus, paraflocculus and vermis, concluding that his views in this regard rest upon insufficient data, in fact upon a (presumably anomalous) hare's brain and are

¹ BRADLEY, O. CHARNOCK. On the Development and Homology of the Mammalian Cerebellar Fissures. *Journ. Anat. and Physiol.*, XXXVII, Jan. and June, 1903.

² Notes on the Morphology of the Cerebellum. *Journ. Anat. and Physiol.*, XXXVII, July, 1903.

not consistent with the data of comparative anatomy generally. And this is followed by a more extended series of notes¹ supplementary to the same author's paper, "The Primary Subdivision of the Mammalian Cerebellum," in *Journal of Anatomy and Physiology* for 1902, and illustrated by a large number of figures, including a useful diagrammatic schema.

C. J. H.

Mendel and Jacobsohn's Jahresbericht.²

The sixth issue of this admirable annual is similar in plan to its predecessors and equally indispensable. It contains 1333 pages, including 61 pages of author's and subject indexes.

C. J. H.

Allis on the Anatomy of the Mackerel.³

This splendid memoir (which has appeared as yet only as an author's separate) follows closely along the lines of the same author's well-known monograph on the cranial anatomy of *Amia*. Indeed it dates from about the same period, having been finished and submitted for publication in July, 1899, and now published without alteration. It is characterized by the same accuracy, thoroughness and beauty of illustration and will doubtless prove a standard of reference for the teleost as the earlier work has done for the ganoid, though one cannot repress a shade of disappointment that it has not been possible for the author to revise the work at the time of publication so as to correlate the findings with the changed conceptions of cranial nerve morphology which the last five years have brought about. For instance, the full significance of the following criticism of GOROXOWITSCH (p. 249) comes out much more clearly now, I opine, than when this was written in 1899: "That a careful study of the course and ultimate distribution of the cranial nerves of fishes can, in the present state of the literature of the subject, have but little morphological importance, and that all important results are to be obtained

¹ SMITH, G. ELLIOT. Further Observations on the Natural Mode of Subdivision of the Mammalian Cerebellum. *Anat. Anz.*, XXIII, 14-15, 1903, pp. 368-384.

² Jahresbericht über die Leistungen und Fortschritte auf dem Gebiete der Neurologie und Psychiatrie. VI. Jahrgang. Bericht über das Jahr 1902. Berlin, S. Karger, 1903.

³ ALLIS, EDWARD PHELPS, JR. The Skull and the Cranial and First Spinal Muscles and Nerves in *Scomber scomber*. Reprint from the *Journal of Morphology*, XVIII, Nos. 1 and 2, April, 1903.

only by a study of the central origin of the fibers, seems to me certainly an error. To know where a nerve goes, and what it does, is absolutely necessary in all attempts to establish its homologies, and is hence equally as important as to know where it comes from, what character of fibers it contains, or how it is developed. Its peripheral distribution should, in fact, be, first of all, definitely known." By way of practical illustration of this contention, Mr. ALLIS has here for another type carried the study of peripheral distribution as far as the most refined dissection methods can do and in some of the cases (such as the relations of the post-vagal nerves) whose interpretation has still baffled him the subsequent microscopical study of these nerves has already solved the problem.

C. J. H.

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PHYSIOLOGICAL EVIDENCE OF THE FLUIDITY OF THE CONDUCTING SUBSTANCE IN THE PEDAL NERVES OF THE SLUG—*ARIOLIMAX* *COLUMBIANUS*.

By O. P. JENKINS and A. J. CARLSON.

(*From the Physiological Laboratory of Leland Stanford, Jr., University.*)

In measuring the rate of the nervous impulse in the slug *Ariolimax columbianus*¹ the fact of the remarkable extensibility of the pedal nerves, which were used for the purpose by us, was a matter of constant observation, as it gave us no little trouble in making the determinations. This slug reaches a large size, individuals being frequently met with which, when extended in the act of crawling, are 25 centimeters in length.

A workable distance of 8 cm. or more of the pedal nerve can be obtained in such slugs. Now this nerve in the uninjured living animal is extended during its act of crawling and contracted during its time of rest and during these changes it, obviously, remains functional. We found that when the pedal nerve is freed from its ganglia and allowed to contract without hindrance it would shorten to about one-half the length maintained in it when the animal was fully extended in the act of crawling. In a muscle-nerve preparation made as described in the paper referred to, this nerve could be repeatedly stretched to this extent and allowed to contract and at each of these positions and at intermediate ones, normal contractions were obtained. Thus the stretching of the nerve through these limits

¹ JENKINS, O. P. and CARLSON, A. J. *American Journal of Physiology*, 1903, Vol. VIII, p. 251-268.

does not appear to affect its functional activity. If, however, the nerve was stretched one or two centimeters in excess of the length it reaches in the animal fully extended by its own act of crawling, this excess of stretching itself acted as a stimulus and both the elasticity and irritability of the nerve were speedily lost not to be subsequently regained. It became a matter of interest to determine what is the effect of stretching the nerve on the rate of conduction of the nervous impulse.

In the time from August, 1901, to May, 1902, the muscle-nerve preparations of 25 individuals, in connection with other work, were tested on this point, and all these showed without exception an increase in the latent period following the extension of the nerve from the contracted state, the height and rapidity of the muscular contraction remaining fairly constant. In order to determine more accurately the relation of the amount of extension of the nerve to its rate of impulse we took a series of records obtained from stimulating the central and peripheral points chosen on the pedal nerve in the contracted condition and in the extended condition. From these records rates for different amounts of extension in the same nerve were determined, allowing comparisons to be made. This series of experiments was carried on at the Hopkins' Seaside Laboratory at Pacific Grove in June, 1902. Except for the alternate stretching and relaxation of the nerve, the apparatus and method of experimentation were the same as used in the previous work on the slug. The muscle-nerve preparations from 16 large individuals in good condition were used and it will be seen from the summary in table IV that several pairs of records both in the extended and contracted condition of the nerve were usually obtained from each preparation.

Fig. 1. Ariolimax columbianus. Four pairs of successive records obtained on stimulating peripheral and central points in the stretched and relaxed condition of the pedal nerve in the same individual. *c.* curve from central, *p.* curve from peripheral point of stimulation.

- | | | | | | |
|--------|------------|------------------|---------|-------|----------|
| No. 1. | Stretched, | length of nerve, | 8 cm. | rate, | 36.8 cm. |
| No. 2. | Relaxed, | " " | " 4 cm. | rate, | 36.4 cm. |
| No. 3. | Stretched, | " " | " 8 cm. | rate, | 33.6 cm. |
| No. 4. | Relaxed, | " " | " 4 cm. | rate, | 30.8 cm. |

4. *Relaxed*

p

c

3. *Stretched*

p

c

2. *Relaxed*

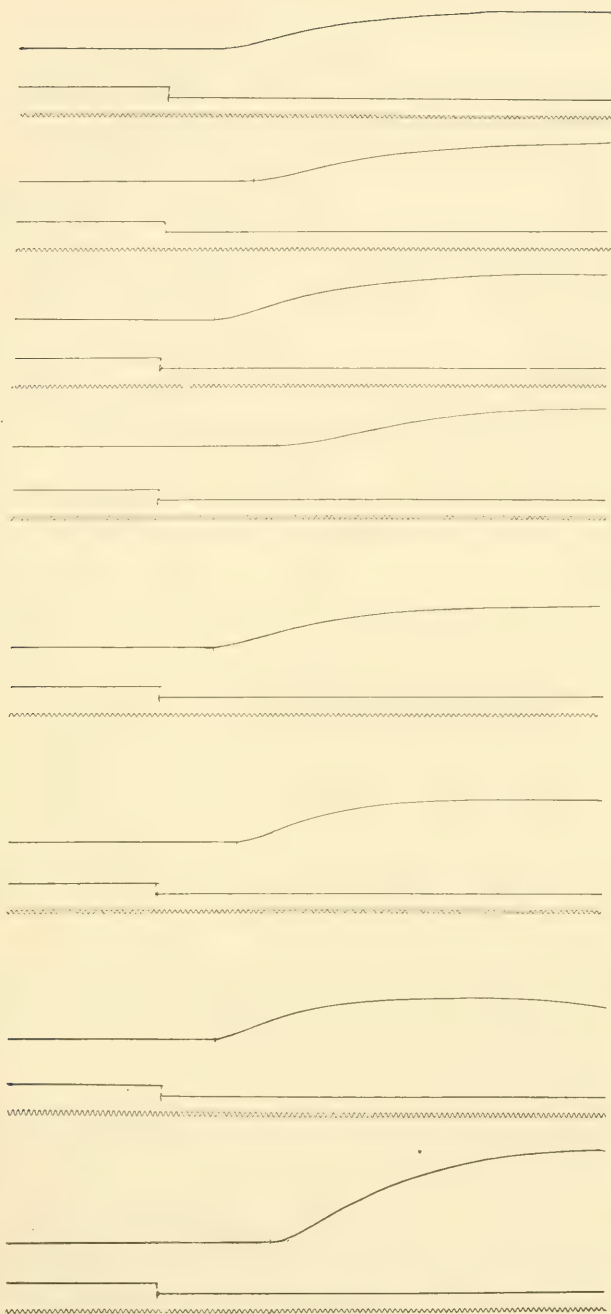
p

c

1. *Stretched*

p

c



To make sure that the point of peripheral stimulation was the same in the extended and the contracted condition of the nerve the point of union of one of the branches with the main nerve trunk was chosen and this point marked with a bit of carbon from the drum which adhered firmly through the experiments. Since the central point of stimulation was in every case nearer the pedal ganglion it was easily kept the same in the two conditions. Although in each of these 16 slugs the nerve was stretched to about twice the length exhibited in the contracted state, in no case was the nerve stretched sufficiently to give rise to an impulse, and it is therefore probable that the degrees of extension of the nerve were within the range employed by the animal in its normal movements. After a second or third repetition of the stretching, the nerve did not always contract to the length first assumed, although freed as much as possible from the restraining force. This was probably due mainly to the viscid mucus in the body cavity which stuck to the nerve more or less and by slightly hardening on exposure to the air, offered some resistance to its contraction.

Of the sixteen experiments three typical ones are given in detail, the remainder only in summary. In this summary (table IV), the "length of nerve," the "transmission time" and the "rate" represent the averages calculated from the individual pairs of records in the stretched and contracted condition of the nerve. Fig. 1 gives a typical series of the tracings obtained from four successive pairs from alternately extended and contracted condition of the same nerve respectively.

A study of these tables shows that there is practically no difference in the actual rate of the nervous impulse in the stretched and the contracted condition of the nerve; the increase in the latent period of the stretched nerve is caused by the additional length of the nerve. In nine of the experiments (Table IV, Nos. 1, 2, 4, 5, 6, 7, 9 and 12) the average rate in the stretched nerve is slightly less than that in the contracted nerve, but, as will be seen from Table I, in these series, individual pairs of records are found which show the reverse. In

TABLE I.

Detail of experiment No. 8, Table IV. June 20, 1902. Temp. 18°C.

Condition of nerve.	Total latent time in seconds.		Transmission time in sec.	Length of nerve in cm.	Rate in cm.
	Central	Peripheral			
Relaxed	0.230	0.136	0.094	4.5	47.7
Stretched	0.428	0.184	0.244	10.5	43.5
Relaxed	0.302	0.160	0.142	5.0	35.0
Stretched	0.524	0.220	0.304	11.0	35.2
Relaxed	0.340	0.200	0.140	6.0	42.6
Stretched	0.580	0.230	0.350	11.5	34.0
Relaxed	0.400	0.200	0.200	7.0	35.0
Stretched	0.590	0.220	0.370	11.5	31.05
Relaxed	0.405	0.180	0.225	8.0	35.2
Stretched	0.595	0.200	0.395	11.5	28.75

Average rate, relaxed: 38.9 cm.

" " stretched: 34.5 cm.

TABLE II.

Detail of experiment No. 13, Table IV. June 23, 1902. Temp. 21°C.

Condition of nerve	Total latent time in seconds.		Transmission time in sec.	Length of nerve in cm.	Rate in cm.
	Central.	Peripheral.			
Stretched	0.314	0.140	0.174	6.0	34.2
Relaxed	0.220	0.104	0.116	3.2	27.52
Stretched	0.360	0.140	0.220	7.0	27.0
Relaxed	0.268	0.120	0.148	3.5	23.45
Stretched	0.380	0.160	0.220	7.0	27.0
Relaxed	0.304	0.134	0.170	4.0	24.0

Average rate, relaxed: 24.9 cm.

" " stretched: 29.4 cm.

TABLE III.

Detail of experiment No. 16, Table IV. June 24, 1902. Temp. 20°C.

Condition of nerve.	Total latent time in seconds.		Transmission time in sec.	Length of nerve in cm.	Rate in cm.
	Central.	Peripheral.			
Stretched	0.470	0.200	0.270	8.0	29.6
Relaxed	0.320	0.178	0.142	4.5	28.4
Stretched	0.740	0.300	0.440	8.5	19.29
Relaxed	0.460	0.220	0.240	5.5	22.50

Average rate, relaxed: 25.4 cm.

" " stretched: 24.4 cm.

TABLE IV.

Summary of 16 experiments on the effect of stretching the nerve on the rate of the nervous impulse in the pedal nerve of *Ariolimax columbianus*.

No. of experiment	No. of pairs of records		Length of nerve in cm.		Transmission time in sec.		Rate in cm.	
	Str.	Rel.	Str.	Rel.	Str.	Rel.	Str.	Rel.
1	3	2	8.0	4.5	0.225	0.105	36.0	44.5
2	2	3	7.5	4.5	0.225	0.126	33.2	35.6
3	3	2	9.0	4.7	0.302	0.166	30.8	30.25
4	1	2	7.0	3.5	0.220	0.094	31.78	36.75
5	4	4	9.0	4.5	0.240	0.108	37.6	41.5
6	3	5	8.16	4.7	0.286	0.146	28.2	32.0
7	3	4	8.66	4.0	0.211	0.096	32.78	44.5
8	5	5	11.2	6.1	0.332	0.160	34.5	38.9
9	3	4	9.3	4.7	0.336	0.139	28.0	36.0
10	1	1	6.0	3.0	0.080	0.040	75.0	75.0
11	1	1	10.0	5.0	0.344	0.170	29.0	29.0
12	4	4	8.1	4.1	0.249	0.120	32.6	36.0
13	3	3	6.66	3.5	0.207	0.144	29.4	24.9
14	2	3	6.0	2.6	0.155	0.079	35.7	34.28
15	4	3	7.5	3.8	0.216	0.126	34.7	30.33
16	2	2	8.25	5.0	0.355	0.161	24.44	25.42

Average rate in the stretched nerve: 34.6 cm. per sec.

“ “ “ relaxed “ : 37.1 cm. per sec.

five experiments (Table IV, Nos. 3, 10, 11, 14 and 16) the rate of the impulse in the two conditions in the nerve is identical, and in two experiments (Table IV, Nos. 13 and 15) the rate in the stretched condition is slightly higher than that in the relaxed or contracted condition. The average rate of all the sixteen slugs is 35 cm. per sec. for the stretched nerve, and 37 cm. per sec. for the contracted nerve. But these differences are slight when one considers the difficulties in applying the peripheral electrodes to exactly the same point of the nerve throughout the successive alternations, and the difficulties in obtaining exact measurements of the length of the nerve, because of the necessary shifting of both pairs of electrodes, not to mention the difficulties in obtaining comparable tracings, due to the unequal relaxations of the muscular part of the preparation. The records leave no doubt in regard to the uniformity

of the rate in the nerve in the different states of extension and contraction within the limits indicated. In the pedal nerves of *Ariolimax*, stretching the nerve within physiological limits increases the transmission time for the whole nerve while contraction or shortening of the nerve decreases it, but in each change of length of the nerve the velocity in a unit of length is the same, that is the rate is the same in the two conditions.

It is obvious that if the change of the length of the nerve was due to the straightening out or the formation of folds and kinks either in the nerve as a whole or in elements in individual nerve fibers the transmission time between two constant points of the nerve would be the same, and the rate would appear greater in the stretched condition as compared to that of the contracted condition. But the fact that the transmission time between any two points increases with the stretching of the nerve seems to show that the stretching is accompanied by actual extension of the conducting substance, whatever that may be. And the fact that the actual rate remains the same in the two conditions of the nerve seems to prove that this rearrangement of the conducting substance does not change the rate of the conducting process. Furthermore, this rearrangement of the molecules of the conducting substance within the wide limits represented by extending the nerve to twice in length does not appear to effect the functional properties of the nerve either in the above experimental conditions or in the normal conditions of the animal.

These facts are certainly evidence on the side of the view that the conducting substance in this nerve is in a liquid condition or at least in a semi-liquid condition.

These experiments also confirm measurements of the rate of the nervous impulse in the pedal nerves of *Ariolimax* reported by us in which the average rate was found to be 40 cm. per second. These records show an average rate of 36 cm. per second, the slightly lower figure in the latter case being in all probability due to the greater number of records used from each preparation, as it will be seen from Tables I, II and III that the rate decreases rapidly during the course of an experiment.

They also show that the particular amount of stretching of the nerve within the physiological limits does not need to be regarded as a source of error in determining the rate of the nervous impulse in this slug.

THE NERVOUS STRUCTURES IN THE PALATE OF
THE FROG: THE PERIPHERAL NETWORKS
AND THE NATURE OF THEIR CELLS AND
FIBERS.

By C. W. PRENTISS,

Instructor of Biology, Western Reserve University.

With 12 figures.

On account of the doubts which have recently been thrown upon the neurone theory by the researches of ΑΡΆΤΗΥ, BETHE and others, especial attention has been drawn to the networks of cells and fibers which apparently form an important part of the peripheral nervous system in most Metazoa.

In his recent book on the nervous system BETHE (:03) discusses at some length the comparative histology and physiology of these structures. According to his own investigations and the observations of HESSE ('95), the brothers HERTWIG ('78), and EIMER ('79), the nervous system of the Medusae is composed largely of nerve cells and fibers which are united into a diffuse network. The neurofibrillae of this network form a basketwork about the nuclei of the cells, and are connected both with muscle-fibers and with sensory organs in the epithelium of the sub-umbrella. SMIDT (:02) describes a sub-epithelial plexus in mollusks; both he and BETHE demonstrated its connection with sensory organs, and according to the physiological experiments of the latter it also sends motor fibers to the muscles.

Among the arthropods similar structures were first observed by HOLMGREN ('95). Later BETHE ('96) described peripheral networks in Crustacea, and his observations were verified by HOLMGREN ('98) and NUSBAUM and SCHREIBER ('97).

In the nervous system of vertebrates networks of cells and fibers have been studied chiefly in connection with the blood vascular system. They have been described by DOGIEL ('93, '98), LEONTOWITSCH (:01), CAVALIÉ (:02), BETHE ('95, :03) and others. BETHE states that such networks are present throughout the whole integument of the frog. They form a close network about the blood vessels and a wide-meshed sub-epithelial plexus. DOGIEL ('98) and LEONTOWITSCH (:01) have carefully studied the networks in the human skin. They assert that connections exist between these structures and the medullated fibers, but their figures do not convince one of this. Their statements have, however, been verified by BETHE (:03) who figures a medullated fiber continuous with a wide-meshed sub-epithelial plexus. In the vertebrate heart also, DOGIEL ('98), HOFMANN (:02) and BETHE (:03) have observed independently a network of cells and fibers surrounding the muscle bundles. This network resembles closely the diffuse nervous system of the Medusae and BETHE maintains that the structures he has seen are undoubtedly of a nervous nature.

It has been stated even recently by certain investigators, that both the cells and fibers composing these networks are non-nervous structures. BARDEEN (:03), among others, has expressed his doubts as to their nervous character; he criticises LEONTOWITSCH and suggests that the whole network described by the latter may be composed entirely of connective tissue. Even if the fibers are nervous structures the cells may be merely sheath cells.

It is important both to the teacher and student of neurology that these doubts be either confirmed or entirely removed. If networks of true nerve cells and fibers really exist in the integument of vertebrates, then the idea that the peripheral nerves originate only from ganglion cells in or near the central nervous system must be abandoned. If, however, the networks are proved to be nothing more nor less than connective tissue structures, the opponents of the neurone theory have lost one of their strongest arguments.

My research was begun in the Physiological Institute of

the University of Strassburg, where I was studying as PARKER Fellow of Harvard University. While demonstrating with methylene blue the innervation of the frog's heart, I obtained several interesting preparations of the nervous elements in the palate, which led me to a further investigation of their structure. This investigation has enabled me not only to verify several points which have been hitherto in doubt, but also to observe new structures which other investigators have either overlooked or have failed to demonstrate.

In the present paper I shall first give evidence from preparations of the normal palate to show that the fibers of the networks described are true nervous structures. And, secondly, from degeneration preparations I shall endeavor to show whether the cells present in these networks are sheath cells or are as truly nerve cells as those of the brain and sensory ganglia.

I. THE NERVOUS STRUCTURES OF THE PALATE.

Preparations were obtained by injecting $\frac{1}{2}$ cc. of a 1% solution of methylene blue (in normal salt solution) into the abdominal vein of the frog. The animals were either rendered passive by the subcutaneous injection of curare, or tied out immovable on the wooden frame shown in figure 8, p. 107. Within five or ten minutes after the appearance of the stain in the integument, the palate with its nerves and vessels was dissected from the roof of the mouth—an easy task, thanks to the lymph-sinus lying beneath the integument. The preparation was then placed epithelial side down, in a flat watch crystal and the exposed surface moistened with the animal's blood while the progress of the stain was watched under the microscope. When the right degree of staining was judged to be obtained, the blood and mucus were rinsed away with normal salt solution and the tissue fixed with ammonium picrate. The preparations were first usually mounted in glycerin, studied in the fresh condition, and important details sketched with the camera lucida. They could then be quickly washed in water, refixed in ammonium molybdate and mounted in balsam. The molybdate method gives much clearer mounts, but has this disadvantage, that the

finer details are often lost by the washing out of the stain in running the preparations up through the alcohols. By studying preparations by both methods I thus did away with the disadvantages of each. Many mounts were made between two cover glasses, allowing the use of an oil immersion from both sides. This is a distinct advantage when whole mounts are employed.

The frog's palate is innervated chiefly if not exclusively by the Ramus palatinus of the seventh cranial nerve (facialis). Each palatine branch (Fig. 1) passes down to the roof of the

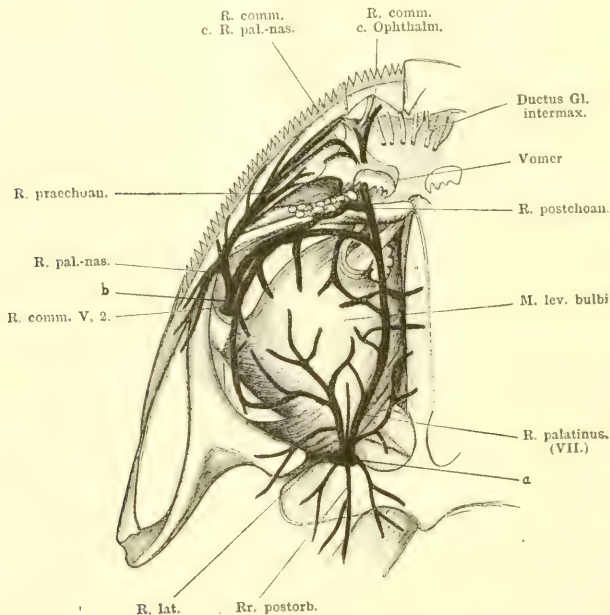
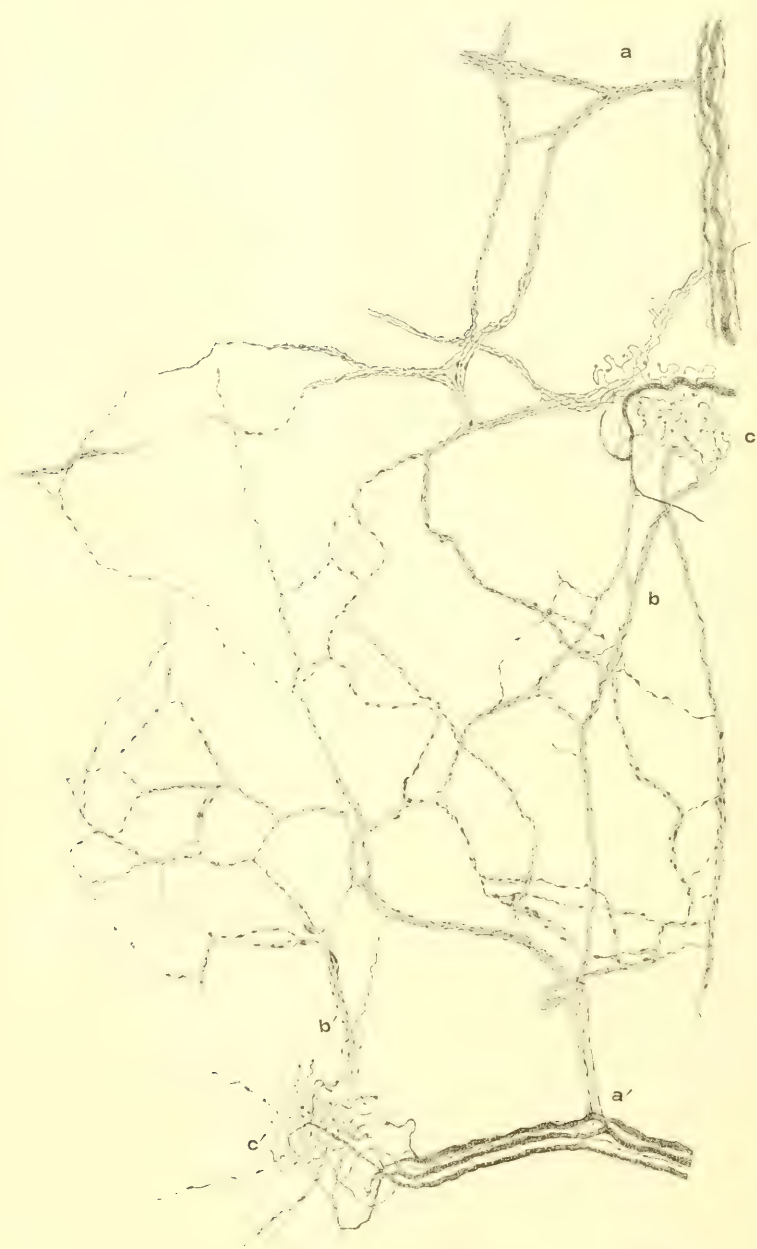


Fig. 1. The roof of the frog's mouth with the integument dissected away to show the course of the palatine nerves. *R. palatinus*, palatine nerve; *R. comm. V. 2*, Ramus communicans of the trigeminal nerve; *a*, *b*, points at which nerve was severed. (After GAUPP).

mouth immediately anterior to the lateral process of the basisphenoid, runs nearly straight cephalad and then, bending sharply laterad, joins the Ramus communicans of the trigeminus. Along its course the nerve gives off many lateral twigs, the fibers of which interlace to form an intricate plexus of medul-

lated fiber-bundles over the whole inner surface of the palate. From this plexus fibers pass off to the epithelium. According to BETHE each medullated fiber divides into four branches and each branch innervates a different sensory organ, the number for each organ being but two. This peculiar and definite method of innervation, he points out, is the most natural arrangement by which each end organ may receive a distinct nerve supply at the expense of the smallest number of nerve fibers—a separate nerve supply for each sensory organ being requisite for the localization of tactile stimuli.

My preparations confirm the general conclusions of BETHE, but the distribution of the sensory fibers is not as simple as he supposed. It is true that usually only two or three large fibers innervate each sensory organ; these break up into numerous fine fibrils, which, after a tortuous course, end between the epithelial cells. The sensory organs in which these fibers end project slightly above the surface of the palate and are most numerous at the sides. BETHE counted an average of 210 end organs but only 70 fibers in the palatine nerve; if each fiber branches into four, as BETHE asserts, this would allow an average of between two and three branches for each sensory spot. But in addition to these branches I find numerous bundles of fibrillae given off from each medullated fiber. These divide into still smaller fibrils which form a network of fine neuro-fibrillae and probably connect the different sensory organs. This network has not to my knowledge been observed in the integument of the frog, but SFAMENI (:02) and RUFFINI (:01) have recently described structures apparently identical to it in the skin of man. In the frog the fibrillae composing the network are very difficult of demonstration. In the great majority of methylene blue preparations they are but incompletely stained, and of good preparations I obtained but two or three out of perhaps a hundred trials. The network lies directly beneath the epithelium and is composed entirely of non-medullated fibrillae (Fig. 2). Strands of these are given off from the medullated fibers as seen in the figure at *a* and *a'*. The strands divide and their fibrils are apparently continuous with each other in a fine-



meshed irregular network; for under a high magnification some of the meshes were found to be formed of a single fibrilla, and it is absolutely impossible to say where one fiber ends and another begins. Certain fibrils from this network end in the sensory spots of the epithelium (Fig. 2, *b*, *b'*); others terminate freely in the regions between the sensory organs. There is thus a diffuse sensory nerve supply throughout the epithelium of the palate.

From certain preparations in which the fibrils of this network were incompletely stained, I was able to trace a single fibrilla from one medullated fiber into another without loss of continuity (Fig. 3). This connecting fibril appears to be homogeneous in structure throughout its entire length. It is very possible that such a condition may be produced by the overlapping of two fibrils. I myself have concluded after a careful study of these networks that they are formed by such an overlapping of two fibrils and not by the direct union of fibrils from different "neurones." In either case it is impossible to say that the fibril belongs to one neurone or to the other.

The presence of fibrillar networks throughout the integument is what we should expect from the physiological facts as to tactile sensations. The whole surface of the skin is more or less sensitive to tactile stimuli but the localization and acuteness of the sensations depend upon the presence of special receptive organs. If two stimuli are applied to a region between sensory spots only one sensation is felt, as the stimulus is diffused and affects equally a number of neurones. If, however, the two stimuli are so far apart as to affect different sensory spots, innervated by distinct nerve fibers, each of these will be strongly stimulated, and two distinct sensations will be the result.

Fig. 2. A subepithelial network of neurofibrillae from the palate of the frog; *a*, *a'*, strands of fibrillae from medullated fibers; *b*, *b'*, fibrillae which apparently end in the sensory spots; *c*, *c'*, two sensory spots. The network is viewed from the epithelial side of the palate, and the terminations of the sensory fibrils among the cells of the epithelium are indicated by knob-like enlargements. $\times 330$; details with LEITZ 1-12 oil immersion.

In addition to this meshwork of sensory fibers there are present in the palate of the frog networks of cells and non-



Fig. 3. A portion of a network similar to that shown in figure 2, with two medullated fibers which are apparently directly connected by a fibril. $\times 1000$.

medullated fibers; these have been observed by BETHE ('95) and are probably identical with the structures described by DOGIEL ('98) and LEONTOWITSCH (:01). For convenience of description a *perivascular* and *subepithelial* network will be distinguished. The perivascular network lies deep in the tissues of the palate and extends wherever blood vessels are abundant. Its meshes are large and the cells comparatively few in number except about the arteries; here a close network is formed by the fibers and many cells are present (Fig. 4). I have observed



Fig. 4. A nerve network about the walls of an artery (frog); a medullated fiber is seen to be connected with this network. $\times 380$.

similar structures in the floor of the mouth, in the upper part of the oesophagus, and in the wall of the intestine. BETHE states that they may be found in all parts of the integument. In many cases medullated fibers may be directly connected with the mesh-work about the arteries. A connection of this kind is shown in figure 4.

I have never been able to make out special endings in the perivascular networks. The nerve fibrils may often be observed

in contact with the circular muscle fibers of the arteries, but no end organs were ever seen at these points.

The network which I have designated as subepithelial is found, as its name implies, directly beneath the epithelium. It consists of a rather fine-meshed plexus of cells and non-medullated fibers; a portion of this network is shown in figure 5.

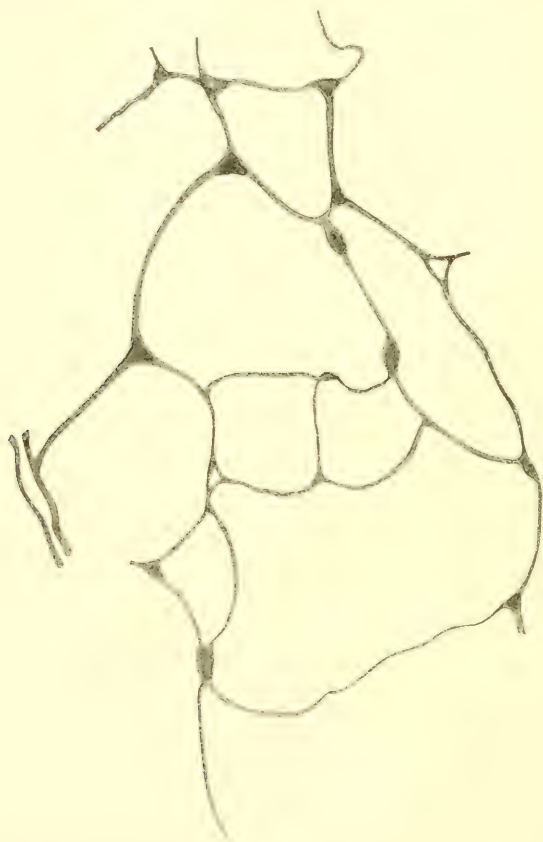


Fig. 5. A subepithelial network of cells and non-medullated fibers from the palate of the frog; the network is continuous with a medullated fiber. $\times 380$.

The fibers seem to radiate from beneath the sensory organs, and at these points from 3 to 6 cells are usually found grouped together (Fig. 11, *a*, *a'*). Into the sensory organs fibers pass from the network, while others are given off at points between

the sensory spots, and end freely in the epithelium. I have never observed fibers from this network innervating the capillaries, but such may be the case. It is, however, connected with the perivascular plexus; medullated fibers also frequently unite with it as may be seen in figure 5. The true nature of these structures has been called into question by many neurologists; I may state here that when I first saw them in my preparations I did not believe that they were nervous structures. After studying them carefully, however, I gathered the following evidence: (1) specific stains for elastic fibers and connective tissue do not demonstrate these networks; (2) as already observed, the fibers of the networks are continuous with branches from medullated fibers; (3) neurofibrillae may be distinctly observed in well differentiated preparations of these networks and the fibers have the varicose appearance characteristic of nerves. In the face of

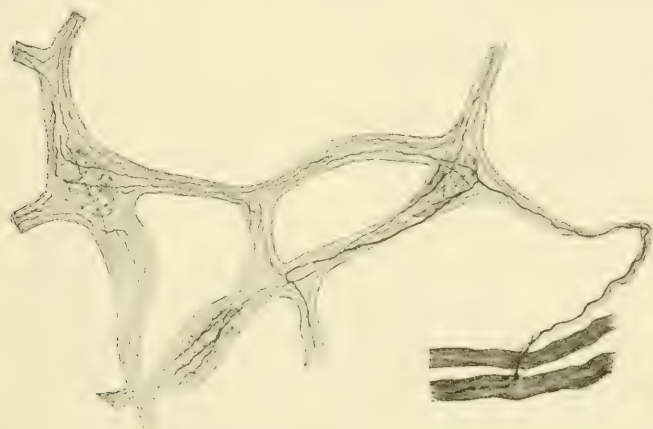


Fig. 6. A group of three cells from the subepithelial nerve network, showing the course of the neurofibrillae, and the connection of a large fibril with a medullated fiber; the fibril branches close to the first nucleus, but no network is formed in any of the cells by the neurofibrillae. $\times 700$.

these facts there can be no doubt that the fibers of both the perivascular and subepithelial networks are nerve fibers. As to the nature of their cells, the histological evidence is no means conclusive. My preparations of the frog's palate do not sustain the observations of BETHE (:03) as to the presence of a neuro-

fibrillar network about the nucleus of each cell. On page 85 he figures two cells showing such perinuclear networks and states in the text: "Von der Existenz glatt durch die Zellen hindurch passierender Neurofibrillen habe ich mich allerdings an diesem Object [palate of frog] nicht mit Sicherheit überzeugen können. Es ist aber doch sehr wohl möglich dass auch hier solche vorkommen, doch ist ihre Zahl sicher nicht gross." To me it seems evident both from BETHE's figures and my own preparations that most of the fibrillae *do* pass directly through the cells. The doubtful point is in the existence of a perinuclear network. The structures figured by BETHE could easily be accounted for by the adhesion of the fibrils at their points of division. BETHE's figures show plainly that the main portion of each fibril passes through the cell. It is only small side branches which show the semblance of a network. Of this I am sure, that in all my preparations of these cells the fibrillae do not form a network about the nucleus. The usual condition found in these cells from the palate of the frog is shown in figure 6. The fibrils often divide in the region of the nucleus, but the branches which thus arise are not continuous with each



Fig. 7. A single cell from the subepithelial network in the palate of *Necturus*; most of the fibrillae run straight through the cell but in the region of the nucleus there is apparently evidence of a network. $\times 1000$.

other. It is possible that the network figured by BETHE may not have been stained in my preparations; but as the fibrillae passing through the cells were clearly demonstrated, it seems strange that some trace of the network, if present, could not

be discovered. In the palate of *Necturus* there was some evidence of a fibrillar basket-work about the nuclei of certain cells (Fig. 7). Only a few meshes were observed and these may have been formed by the crossing of fibrillae; by far the greater number pass directly through the cell without branching, as may be seen in the figure. I therefore maintain that these cells, if nervous structures, are to be compared, not as BETHE would have us, to the ganglion cells of invertebrates (in which a complete basket work is formed by the fibrillae), but rather to the central nerve cells of vertebrates, through which, as a rule, most of the neurofibrillae pass entirely independent of each other.

In the palate of the frog the cells of the networks are usually located centrally with reference to the fibrillae, the nucleus being surrounded by the latter. It is difficult to see how such nuclei can be interpreted as belonging to sheath cells. Often, however, a cell lies eccentric to the fiber, the fibrillae all passing to one side of the nucleus; or two nuclei may be found in close proximity to each other, the one surrounded by fibrillae, the other being eccentric in position. The form of the nuclei also varies with their location. If surrounded by fibrillae the nucleus may be of spheroidal or pyramidal shape; if lying eccentric they are usually flattened and elongate in form.

I have described in some detail these networks of cells and fibers both because my observations substantiate more or less completely the results of DOGIEL, BETHE, and LEONTOWITSCH, and in order that the significance of the following degeneration experiments might be more easily understood. From the histological evidence one must conclude that the non-medullated fibers of all these networks are true nervous structures, and not connective tissue as has been maintained. They are composed of neurofibrillae, are connected with medullated fibers, and are not demonstrated by specific connective tissue stains. The presence of neurofibrillae about the nuclei of some of the cells would indicate that they also are of nervous character, as BETHE and LEONOWITSCH assert. The evidence as to the presence of neuro-fibrillar networks in these cells is not conclusive,

and those eccentrically located might well be sheath cells. The nature of these cells therefore is not definitely settled, and is a problem of great importance. For if it is conclusively proved that they are nerve cells, the structural independence of the neurone and its genesis from a single ganglion cell can no longer be maintained. By a series of degeneration experiments I have attempted to solve the problem.

2. THE RESULTS OF DEGENERATION EXPERIMENTS.

If all of the nerve fibres in the palate of the frog are processes of the nerve cells situated either in the brain or in the sensory ganglion of the seventh cranial nerve, they should, when isolated from these cells for some weeks, degenerate completely, being separated from their only trophic centers. If, however, there are peripheral nerve cells in the palate, these as well as the fibers connected with them should remain histologically unchanged. To determine which of these assumptions is correct the following method suggested itself: To sever the palatine nerves from all connection with their central cells, and after the expiration of a period sufficient for complete degeneration, to attempt the demonstration of the peripheral networks by means of methylene blue. The chief difficulty connected with this method lies in the well known fickleness of the stain, a factor which might lead to negative results. I therefore experimented with normal animals until I was able to obtain regularly a good percentage of successful preparations. It was found that the subepithelial and perivascular networks take the stain very quickly as they are in close proximity to the blood vessels and capillaries, through the walls of which the stain passes to the other tissues. The chief point in getting good preparations therefore, is the removal and fixation of the tissues as soon as possible after the stain has passed through the capillaries. If one waits until the larger nerves are impregnated, the color will have disappeared from most of the finer elements.

As is well known, methylene blue is a specific stain for degenerated myelin, and BETHE has proved that the neuro-

fibrillae, when degenerate, lose their power of taking up the stain. In methylene blue preparations it is therefore easy to distinguish between normal and degenerate nervous structures.



Fig. 8. Photograph showing operating frame, the method of tying the frog and the point at which the root of the palatine nerve was exposed. About $\frac{1}{2}$ nat. size.

The palatine branch of the seventh nerve passes, as we have already seen, to the roof of the mouth directly anterior to the lateral process of the basisphenoid bone (Fig. 1, page 96). Lateral to the eyeball it is connected with the maxillary branch of the fifth cranial nerve by the *Ramus communicans*, although, as far as I have been able to discover, no fibres from the trigemus innervate the palate. To make sure however, that the

palatine nerve is completely isolated from the brain and sensory ganglia, it must be severed at the points *a* and *b*.

The operation is simple and may be performed in the following manner. The frog is tied out back down upon a wooden frame nine inches long, shaped as shown in figure 8. In each of the five extremities of this frame a vertical slit has been cut. Three small blunt hooks attached to ten inch lengths of thread were provided. The mouth of the frog is opened, a hook caught into the upper jaw and the string drawn taut through the anterior slit, as seen in the figure. By means of a second hook the lower jaw is drawn back against the sternum and the cord fastened in one of the posterior slits. The animal is thus held motionless with mouth wide open. With small scissors an incision one-fourth inch long is made along the median line of the palate. One edge of the cut is then carefully lifted with forceps and hooked to one side, the string being drawn through one of the lateral slits. This exposes the palatine nerve at the point where it enters the roof of the mouth. (Fig. 1. *a*; Fig. 8). Next a small hooked needle may be passed under the nerve, the blood-vessels separated from it and a portion of the nerve removed. Both palatine nerves may thus be severed by making but one incision, and if the operation is carefully performed, without the loss of a drop of blood. In a similar manner the Ramus communicans may be cut at the point *b* (Fig. 1) by making two small lateral incisions. It is not necessary to sew up the incisions; in fact the thread used in the stitches was found to irritate the animals and in most cases the edges of the wounds were simply drawn together.

Degeneration Experiments.

Series 1. This series of operations was practically negative in its results. Eight animals were operated on during the last week in June, 1903. Six died, before the expiration of two weeks, of a skin disease which developed upon all the frogs kept in the laboratory at the time. Of the two surviving individuals only one took the stain, and in this case very incom-

pletely. In the fresh preparation there was some evidence of the subepithelial network, but after fixation the stain was too faint to demonstrate clearly the difference between degenerate and non-degenerate nerves. I was encouraged, however, to make further attempts.

Series 2. During the first week in October 1903, twelve frogs were operated upon. Of these three survived twenty-one days and were injected with methylene blue. Again only one palate took the stain well. In this preparation a network of non-medullated fibers was clearly demonstrated, and there was some evidence of it in one of the other preparations. BETHE (:03) has shown that when the peripheral nerves of winter frogs are cut distal to their cells, the neurofibrillae of the axis cylinders lose their affinity for stains after the expiration of from twenty-one to twenty-four days. This he proves to be due to the disappearance of the organic substance (Fibrillensäure) which is a constituent of all normal neurofibrillae and which, combining with certain dyes gives the primary fibrillar stain of both nerve cells and fibers. The fibrillae lose this acid substance, and refuse to stain long before myelin sheaths of medullated nerves show signs of degeneration. In these preparations of the palates in which the nerves have been cut for three weeks, the myelin sheaths had almost completely broken down, showing constrictions and vacuolations throughout the course of the fibers. This does not agree with results of BETHE and MÖNKEBERG ('99) who found complete degeneration of the medullary sheaths in the frog only after a lapse of 102 days, although the neurofibrillae had lost their specific staining power within three weeks. I therefore conclude that the process of degeneration must either proceed much more rapidly in the nerve fibers of the palate than in those of the sciatic nerve, or that the period of nerve degeneration is much shorter in the autumn than during the winter months. To make sure that degeneration was complete, a third series of frogs was operated upon.

Series 3. On November 3rd, 1903, the palatine nerves of six individuals were severed. Three of these frogs were kept alive for thirty-five days and two good preparations of the pal-

atine nerves were obtained. The stain was unusually complete for methylene blue preparations; the trunk and branches of the palatine nerve, the plexus of medullated fibers, and the branches running from this plexus to the sensory organs, were all demonstrated. But, while in methylene blue preparations of normal nerves the myelin sheaths are colorless and the axis cylinders (especially at RANVIER'S nodes) are deeply stained (Fig. 3), in these degenerate nerves it is exactly the reverse. The stain is limited entirely to the myelin substance, and the axis cylinders are not demonstrated, a characteristic staining reaction for degenerated nerves. This is the case not only in the larger branches of the palatine nerve but also in single peripheral fibers (Figs. 9 and 10). Even without high magnifi-

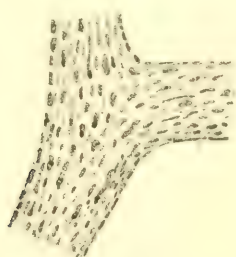


FIG. 9



FIG. 10

Fig. 9. A portion of a medullated nerve from a frog's palate, the nerves of which had been severed 35 days before the preparation was made; the dark granules are the remains of the myelin sheaths; the axis cylinders of the fibers are not demonstrated. $\times 360$.

Fig. 10. The distal portion of a single medullated fiber from the same preparation as Fig. 9; the myelin sheath is broken up into irregular segments which are deeply stained. $\times 700$.

cation it may be seen that the disintegration of the myelin sheaths is complete (Fig. 9). The myelin has broken up into short segments which are deeply stained, the nuclei of the sheath have apparently disappeared and the nodes of RANVIER cannot be recognized. Comparing a single degenerate fiber from one of these preparations (Fig. 10) with a normal medullated fiber (Fig. 3) the difference can be seen at a glance. Not a single normal medullated fiber was found in the large nerve

branches supplying the palate. Furthermore the endings of the medullated fibers in the sensory spots of the epithelium were not demonstrated, endings which, under normal conditions, are almost always stained.

It is clear from such preparations that isolation from the central nervous system was completely accomplished by the operation. For the medullated fibers of the palatine nerves were not only wholly degenerated, but also stimulation of the isolated region failed to call forth any response. According to BETHE the myelin substance does not begin to undergo degeneration until some time after the axis cylinders have lost their staining properties, and it follows that the latter have been degenerate for a considerable period. But is this the case with the non-medullated fibers of the peripheral networks which BETHE and others have asserted to be directly connected with true nerve cells?

In every degeneration preparation of the palate methylene blue failed to stain the fine network of the sensory fibrillae which I have described and shown in figure 2. This result was to be expected, as the network consists only of non-medullated fibrillae, all branches of medullated fibers, and goes to show that the degeneration of the latter is complete. But in both cases in which the palatine nerves had been isolated for five weeks the subepithelial and perivascular networks were beautifully stained. Neither fibers nor cells showed the least trace of degenerative changes. In regions where the stain was well differentiated the neurofibrillae could be easily made out, proving that these elements were in a normal condition, and that the staining of the fibers was not alone due to the impregnation of the perifibrillar substance.

A portion of the subepithelium network from one of the preparations of *series 3* is shown in figure 11. It will be noted that a number of cells are grouped together at the points *a* and *a'*. The spot where such a group of cells occurs is in every case immediately beneath a sensory organ, and the fibers radiate out from these regions. Certain fibrils pass from the cells and apparently end in the sensory organs. I was not able to settle

this point definitely but there are other fibrils which end in the epithelium between the sensory spots. From this it is evident that a part at least of the fibrillae of this network are sensory in function. And it is not clear to me why the cells should be grouped together beneath the sensory organs unless they have some connection with them.



Fig. II. A portion of a subepithelial network from a degeneration preparation (period of degeneration five weeks); the cells and fibers apparently show normal structure, and were normally stained. *a, a'*, groups of cells beneath sensory organs; *b, b'*, degenerated medullated fibers of which *b* is connected with the network; *c*, a medullated fiber continuous with the network and showing normal structure for a short distance at its distal end. $\times 225$.

It has already been shown that certain of the fibers of the subepithelium network are directly continuous with medullated nerves. In the figures two such cases are seen; at times such fibers could be traced a considerable distance along the degenerate nerves of the medullated plexus. These fibers showed all the normal characteristics of medullated nerves, but were never observed in the large nerve trunks. Other medullated fibers connected with the subepithelial network showed degenerative changes up to the point where they lost their myelin sheaths. As far as observed the only normal medullated fibers to be found in these degeneration preparations, were those connected with the subepithelial network. This network was found stained in all parts of the palate. The perivascular networks were not so completely demonstrated, but this was probably due to incomplete staining rather than to the degeneration of the networks about the vessels. For these networks are never completely stained in normal preparations. When stained in the degeneration preparations, neither fibers nor cells of the perivascular network show histological differences when compared with normal preparations (Fig. 12). As far as structure and staining qualities go, the one cannot be distinguished from the other.



Fig. 12. A portion of a nerve network about the walls of a small vessel; from the same preparation as figure 11. $\times 360$.

These series of degeneration preparations prove therefore that the peripheral networks of fibers and cells will retain their normal structure after five weeks of isolation from the central ner-

vous system. The objection may be raised that the period which elapsed was not long enough, that the degeneration was simply incomplete, that the distal endings of the fibers form the networks and that these were still in their normal condition. But we have already seen that the distal endings of most of the medullated nerves, the terminal fibrillae in the sensory organs, have completely degenerated. Why do the fibers of the networks alone fail to show similar changes?

It has been shown in the first part of this paper that the fibers of these networks are nerve fibers. It cannot be maintained therefore that they do not degenerate because they are non-nervous structures. The only explanation of their immunity from the degenerative changes which affect the isolated medullated nerves is that the cells of the network exert upon them a distinct trophic influence. The cells are then something more than sheath cells or connective tissue cells as BARDEEN and others have asserted. The medullated fibers of the palate are well supplied with sheath cells but this does not prevent their degeneration when separated from their ganglion cells. We can only conclude that the cells of these networks are true nerve cells in that the integrity of the fibers is dependent upon them. This is in strict agreement with the conditions which we find in the nervous system of the lower animals, and substantiates the conclusions of BETHE and LEONTOWITSCH.

As to whether these networks of nerve cells and fibers will retain their integrity indefinitely when severed from all connection with the central nervous system, we do not know at present. Experiments are in progress to determine whether they also will degenerate in the course of a few months, or whether they possess the power of regenerating new fibers. BETHE (:03) maintains that the sheath nuclei are modified nerve cells and still retain their primitive function of neurogenesis. It might be expected that these peripheral nerve cells possess a similar function. Our present data are not sufficient however to warrant the assumption of LEONTOWITSCH that there is a constant process of physiological regeneration going on in the skin, and that the subepithelial network is transformed into the

peripheral portion of a neurite from a sensory ganglion cell. It seems to me rather that in these networks of nerve cells and fibers we have to do with primitive nervous structures more or less independent of the central nervous system, structures which, as BETHE points out, correspond to the diffuse nervous system of many invertebrates, and which are connected, on the one hand with the integument, and on the other hand with the non-striated musculature.

SUMMARY.

1. The palatine branch of the seventh cranial nerve forms a plexus of medullated fibers in the palate of the frog; from this plexus fibers pass, to end by branching in the sensory organs of the epithelium.

2. The innervation of the sensory organs of the palate is not as diagrammatic as has been asserted; a diffuse network of neurofibrillae connects different sensory neurones, and puts the sensory organs into communication.

3. A network of cells and non-medullated fibers extends throughout the deeper layers of the palate and forms a close meshwork about the walls of the vessels.

4. Immediately beneath the epithelium is found another network of cells and fibers; sensory fibrils from it end in the epithelium, and it is also connected with the perivascular network.

5. The fibers of the networks are nervous structures for (a) they are not demonstrated by specific stains for elastic and connective tissue; (b) they are composed of neurofibrillae; (c) they are often directly continuous with medullated nerves.

6. Neurofibrillae are present in the cells of the networks, but most of them pass through without forming a basket-work about the nucleus.

7. When the nerves of the palate are isolated from their ganglion cells the medullated fibers which end in the epithelium degenerate at the expiration of 25 to 35 days; the myelin sheaths disintegrate, and the axis cylinders fail to stain.

8. Under the same conditions both the cells and fibers

of the subepithelial and perivascular networks stain in a normal manner and show no degenerative changes in their structure.

9. Some of the cells of the network are therefore true nerve cells and exert a trophic influence upon the fibers connected with them.

10. The networks are comparable to the diffuse nervous system of certain invertebrates, and their existence is incompatible with the idea that the nervous system is composed of of distinct cellular units.

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THE BEGINNINGS OF SOCIAL REACTION IN MAN AND LOWER ANIMALS.

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It seems to be easy to employ the word "social" in a very slipshod manner and it may very well be that greater care in its definition would remove several bones of contention that are being worried from time to time in the journals.

When we admit that human experience "polarizes" (to use Professor BALDWIN's expression) into *ego* and *alter* extremes, it becomes necessary very carefully to guard what is meant by the social self or social consciousness. CLIFFORD, and other writers since, have written of a tribal conscience or tribal self. Such expressions may easily be interpreted as though society were possessed of a consciousness in the same sense that the individual is. Now this is, of course, nonsense, or rather, a frequently exposed fallacy.

When we speak of the social self we mean the social reflected in the individual or else we mean an abstraction of common elements in the individual selves constituting the society, which common factors we may thereafter use, like an algebraic expression, as though it had an independent existence. It would be of immense advantage in simplifying philosophical and anthropological inquiry if some sort of an agreement could be reached as to the use of words in this connection. Ought we not carefully to distinguish the two elements just referred to? Let us, for example, call the first the "socius consciousness," meaning thereby all that portion of our conscious acts which involves the recognition of other-in-self and self-in-other, or if the line cannot be drawn, our conscious acts in so far as this implication is under consideration. Let the second element be

termed "society consciousness," meaning thereby the common elements in the consciousness of the constituents of society or the *consensus* of society. In this way we avoid the ambiguity of the term social consciousness, or, if that term must be used, then by all means limit it to the social reactions within the individual consciousness and use the necessary circumlocutions to express the consensus idea.

Professor BALDWIN, in his genetic series, lays great stress on the "bipolar self." He shows that development of the *ego* goes *pari passu* with that of the *alter*; that self is social from the start. But this is only a phase of the general psychological law that self is reflexive. The wave of effort is met by an inflowing wave of resistance. Without both of these elements experience would be impossible. Just as the simplest form of subjectivity is coupled necessarily with an objectivity (substance), so the most rudimentary personality involves the social element.

For ethical purposes it is necessary to note that every moral act or thought has a social implication. This is part of the meaning of KANT'S well-known rules of morals. But psychology has, or ought to have, something to say as to the origin of the social faculty. Much of this has been interpreted by Professor BALDWIN in his description of the projective and ejective stages of social development.

Perhaps, however, some attention should now be given to the condition back of the projective activity, namely to the continuum habit, or, negatively expressed to fit its more common manifestation, the *hiatus effect*.¹ If the equilibrium theory of consciousness be true, the elements in the equilibrium may be roughly classified into relatively constant, and variable elements, the a, b, c, series and the x, y, z series respectively.

By a process of familiarization, one of the variables may be converted into a constant and become a part of the usual furniture of consciousness. The process of assimilation causes the stimulus or group of stimuli increasingly to participate in

¹ The law of dynamogenesis is implied throughout.

the self group. A wooden leg or a thorn in the flesh may assimilate itself closely to the self of normal experience, self being, of course, a relative or variable term the center of which alone is fixed.

Now let any circumstance deprive us, let us say, of any "a" in the series of constants and there at once arises what we may call a feeling of hiatus. If this is true of stimuli in general, it is no less true of many stimuli that are called social. The habitual reaction to the expected resistance is a large part of our daily activity and holds the germ of social response. If the very trivial nature of the following illustrations can be forgiven they will illustrate what is meant better than psychological discussion.

The writer has two horses which for years have been driven, housed and fed together. All habitual activities have been coordinated by necessities growing out of their environment. Originally the animals (mares) regarded each other with distrust and even hostility. Even after years, their intercourse is always aggressive. One steals the other's feed and is attacked for it. There is a continual "nagging." Usually one acquires the ascendancy and all that is necessary is a show of teeth on the part of one to cause flight or submission on the part of the other, which, nevertheless, is in a state of constant rebellion.

Now should one animal be left in the stable with a manger full of hay and the other driven away, the stay-at-home is restless and uneasy, declines to eat and neighs continually. The animal driven away strives to turn back, is nervous and neighs and starts out of the road on coming in view of any horse in the distance. Each, as we say, "misses" the other. What is the explanation? Evidently the simplest explanation is that a large segment has been knocked out of self. A whole group of activities (resistances and the like) have been removed. The equilibrium of habitual activity has been disturbed. For weeks every act has been tacitly or by unconscious implication put forth in view of a presence which could be relied upon to react in certain ways. Hitherto the horse never ate, drank or pulled

in harness without expecting a certain set of counter actions. These may have been unpleasant reactions. When she drank she expected to be shoved aside, when she pulled she expected to be tweaked by her fellow. But, whatever the character of these acts, they have ceased; to the action the wonted response is wanting.

One gets this sense of hiatus in an elementary form when, in climbing a ladder in the dark, a rung is discovered to be missing. Again, we return to the home after sending the family away on a picnic, thinking "how pleasant it will be to have a quiet day in the study" and find that the unwonted quiet sends us wandering through the empty house seeking we know not what that has gone from our life and the working equilibrium is not soon restored. This is the "feeling of hiatus." It is not confined to animate objects. The writer was once disturbed to find that he could not work well—things were not going as usual—there seemed to be a kind of mental unbalance and he discovered the cause in the fact that he had forgotten to put on collar and tie. This hiatus filled, the typewriter seemed to have as free a play of thought as ever. Certain fussy authors and artists have found it impossible to compose except in full court dress. (I fancy a disembodied spirit would have some difficulty at first with his "hiatus.")

The infant, when passed from the arms of the nurse to those of a stranger, notices the difference and shows fear or discomfort. A strange room also disturbs the equilibrium of experience. The sphere of experience created by every individual is normally a "continuum." When this continuum is disturbed the ensphering environment is left incomplete and one has the same sensation he has when the support beneath him is knocked out. It is not necessary that there should be any intellectual status in the intercourse.

The above seems to be the most elementary condition of social existence. It consists in the enlargement of the sphere of experience by the admission of more and more elements which acquire a value to my being as a part of the equilibrium quite independent of any moral element in it. Its removal pro-

duces an emotional reaction growing out of the feeling of loss—hiatus in self—solution of individual continuity. We here have the elementary mechanic of social life.

It is only after this relation is *perceived as mutual* that a moral element enters. When the child was about to leave home for a long visit he visited the cow, the chickens, and the cat to say farewell, and his regret in parting was greatly enhanced by the feeling of how great the grief of these fellow creatures must be in losing him. He even paid a visit to familiar spots and took leave of them with all the feeling of reciprocity that he experienced in the case of living things. These things formed a real part of his experience, he must also form a part of theirs. This feeling of participation is a second step and a moral one. This phase of social feeling is never entirely obsolete. "Who shall smoke my meerschaum pipe" and "these dear spots shall see me no more" illustrate this fact.

Add the further idea of dependence and a high social status is reached. "Really, I ought not to go away, for the servant will forget to feed the animals." Obligation has arisen because of the feeling of participation. I find that I form a necessary segment in their lives, and, as they form a part of my sphere—of "me"—of my larger or social self, I am obligated by that fact, i. e., by an enlargement of the law of self-preservation, to care for these animals. This is an obligation having a different kind and more intimate sort of compelling force than would be possible in the case of an inanimate and so non-participating thing. It may be that in reality the animals do not know that they are dependent on me for their sustenance, but it suffices that I imagine them so to feel. This mutuality feeling makes the obligation moral in a different sense from that growing out of fear that I might perhaps suffer a pecuniary loss by neglect.

It is customary to say that the social self is ejective, i. e., that we project our own feelings and experiences into others and act in view of them. Another and in some respects a truer way of expressing it is that the self is constantly enlarging to embrace new elements. It is not simply that someone else feels as I do—that might be an interesting fact, but it would have no

compelling power. It is rather that I affect the other who partakes with me in feeling. My affecting him makes him partner in my feeling. It is the element of participation or recognition of self in other which creates obligation. The mere fact that men in Mars feel as we do would not awaken moral response unless it could be showed that we affected them in some way.

Professor FISKE has indicated that the long period of helplessness on the part of the human infant is a very important factor in the intellectual superiority of the individual human being. Still more important to the race is the effect of long-continued dependence on the development of society. The tie that binds early societies is to a very large extent this same helpless period of infancy. In most lower animals this period being very short, the family relation covers a very limited period, while in the human family under ordinary circumstances this dependence is a continuing state and the family (and so eventually the tribe) becomes a permanent element to be reckoned with in all dealings with men.¹ It is not necessary to point out the many and far-reaching results of this fact.

¹ Note that social insects likewise pass through a helpless stage, requiring active "nursing."

INHIBITION AND REINFORCEMENT OF REACTION IN THE FROG *RANA CLAMITANS*.

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GENERAL PROBLEMS AND METHODS.

An investigation of the time relations of neural processes in the frog, which began with the determination of simple reaction-time (YERKES, '03, p. 598 et seq.), has now been extended to a study of the influence of complication of stimuli on time of reaction. In this report an attempt will be made to present, in summary, certain results which contribute somewhat to our knowledge of inhibition (*Hemmung*) and reinforcement (*Bahnung*).¹

Attention was called, in the paper referred to above (p. 627 et seq.), to the inhibition, by visual stimuli, of visible motor reactions to auditory stimuli, as well as to the apparent reinforcement, by an auditory stimulus (tuning-fork sound), of reactions to visual stimulation by a moving red disc. These observations led to a more detailed and systematic study of the influence of complication of stimuli, so far as reaction-time is concerned.

The work thus far done includes studies of (1) the effect of stimulation by increase in light intensity upon reaction-time to electric stimulation of the skin, (2) the effect of an auditory stimulus upon electric reaction-time, (3) the effect of visual stimulation by the appearance of a moving finger, (a) when shown almost simultaneously with the giving of the electric stimulus, and (b) when shown a considerable interval (at least

¹ This work will be published in detail, in connection with other results, in Volume 2 of the Harvard Psychological Studies.

one second) before the giving of the electric stimulus, (4) the effect of visual stimulation by a moving red disc, shown in one series of experiments 0.1'', and in another 0.5'' before and until the electric stimulus was given.

In all cases the reaction-time to electric stimulation of the skin was studied with special attention to the influence of other stimuli which were given in definite temporal relation to the electric stimulus. The general method of the investigation was the same as that described in my earlier paper (p. 601). A Hipp chronoscope, controlled by a Cattell's falling screen, served as a time measuring apparatus. The other essentials of the apparatus were a reaction-box, and devices for giving the stimuli and indicating the reaction. On the bottom of the reaction-box a series of wires were so placed that an electric stimulus could be given to the frog resting upon them by the closing of a key in the hands of the experimenter. In preparation for each experiment the frog was placed upon these open circuit wires in such a position that the weight of its body pressed upon a delicate spring in the floor of the box, thus causing the chronoscope circuit to be completed. The forward jump of the frog in response to stimulation caused the breaking of this circuit by the release of the spring upon which the animal rested. When all was in readiness for an experiment the chronoscope was started, and a key closed which simultaneously gave an electric stimulus to the frog and completed a circuit which caused the chronoscope record to begin. The stimulus consisted of a current from one or more "Mesco" dry batteries. The motor reaction of the frog broke the chronoscope circuit, thus causing the chronoscope record to stop. It was then possible for the experimenter to read from the dials of the chronoscope the time, in thousandths of seconds, intervening between stimulus and reaction (reaction-time). In case of additional stimuli in connection with the electric, various simple devices were introduced to meet the demands of the experiments. These will be described in connection with the statement of results in each case.

RESULTS OF EXPERIMENTS.

1. Electric Stimulation and Light.

The following specimen records leave no room for doubt as to the inhibitory influence of increase in light intensity on the electric reaction. In these tests the visual stimulus was given from 1 to 2 seconds before the electric by the turning on of a 16-candle power electric light which was placed 30 cm. in front of the animal in one series, and 15 cm. above it in another.

The laboratory records appended are self-explanatory.

TABLE I.

Title of investigation. . . . Electric-Visual Series (Red Light).
 Experimented on. . . . Green Frog No. 4.
 Harvard Psychological Laboratory. . . 9.15 A. M., Feb. 28, 1902.
 Chronoscope control average 189 σ^1 . . . Electric stimulus, 1 Cell.
 Red light, 16 c. p., 2 seconds before and until electric stimulation.

Number of Experiment.										Reaction-time.
1	144 σ^1
2	192
3	587
4	No reaction.
5	No reaction.
6	Reaction to second stim.
7	No reaction.
8	No reaction.
9	177
10	No reaction.
11	No reaction.
12	No reaction.
13	No reaction.
14	1190
15	No reaction.
16	No reaction.
17	No reaction.
18	No reaction.
19	No reaction.
20	No reaction.

Table I indicates the lack of response to a 1 cell electric stimulus when accompanied by an increase in light intensity, and Table II proves conclusively that the light is the cause of the inhibition of reaction.

¹ All reaction-times are given in thousandths of a second, indicated by σ .

TABLE II.

Title of investigation. . . . Electric-Visual (Red Light).
 Experimented on. . . . Green Frog No. 4.
 Harvard Psychological Laboratory. . . . 9.40 A. M., Feb. 28, 1902.
 Chronoscope control average, 189 σ Electric stimulus, 1 Cell.

No LIGHT.							
Number of Experiment.							Reaction-time.
1	152 σ
2	145
3	221
4	327
5	263
6	271
7	329
8	215
9	225
10	216
LIGHT BEFORE ELECTRIC STIM.							
11	No reaction.
12	No reaction.
13	No reaction.
14	No reaction.
15	No reaction.
No LIGHT.							
16	216

The inhibitory influence of light in this case depends upon the intensity of the electric stimulus. Even a very strong light will not cause much retardation of reaction to a 3 or 4 cell current. As the strength of the electric stimulus decreases the delay of reaction increases, until finally there is complete inhibition. At this point, an electric stimulus to which the frog would react almost invariably when there is no disturbing condition, will fail to cause reaction in the presence of a sudden increase in light intensity.

MERZBACHER ('00, p. 253) states that the leg reflex of a frog, so placed that its legs hang free in the air, is greater in response to a given cutaneous stimulus in darkness than in daylight.¹

¹ "Blendung oder blosse Lichtentziehung erhöht die Erregbarkeit für mechanische Reize." (p. 253.)

2. Electric Stimulation and Sound.

Inasmuch as the experiments here described were conducted in a laboratory where noise and jar are unavoidable, it is worth while at this place to offer reasons for the belief that sounds did not to any considerable extent affect the time of reaction to other stimuli.

As tests of the influence of loud sounds on the electric reaction-time, an apparatus was arranged whereby an electric bell rang for a certain interval before the electric stimulation. The bell was placed 40 cm. from the frog, and for one series of 300 reactions it rang 0.1 second before the electric stimulation, for another 1.0 second before. The reactions were taken in pairs, first a reaction to the electric stimulus alone, then one to the electric stimulus preceded by the auditory, at the rate of one a minute. The results may be summarized, without mention of other values than the means, thus:

Series I.	{	Average of 300 reactions to 2 Cell Electric Stimulus Alone, 172.0 σ
		Average of 300 reactions to 2 Cell Electric Stimulus, when preceded for 0.1 second by Auditory Stimulus, 176.5 σ
Series II.	{	Average of 300 reactions to 2 Cell Electric Stimulus Alone, 144.7 σ^1
		Average of 300 reactions to 2 Cell Electric Stimulus, when preceded for 1.0 second by Auditory Stimulus, 150.2 σ

In each of these series there is evidence that the sound caused slight inhibition or delay of reaction, but when we consider, as will be made clear later, that the probable error of the averages is greater than the apparent delay, it is at once evident that we can not safely argue from these results to the inhibitory influence of sound. Indeed most observations on record tend to show that audition is not very important in the frog, at least when it is out of water.

3. Electric Stimulation and Moving Object. Preliminary Experiments.

For the purpose of determining the effect upon reaction-time to an electric stimulus of stimulation of the eye by a

¹ The conditions were not precisely the same for the two series, as the frogs had become inactive.

rapidly moving object, experiments were made in which, as in the case of sound and electricity, reactions to the electric stimulus alone and to visual and electric were alternated. Thus in case of each pair of reactions it was possible to note whether the visual stimulus lengthened or shortened the reaction-time. The visual stimulus was given by quickly bringing a finger before a window in the reaction-box.

As a preliminary test two series of 20 pairs of reactions each were taken with two frogs (Nos. 5 and 6). In the first series the finger was suddenly moved over the window, and the electric stimulus was given either simultaneously or a small fraction of a second later. It was of course impossible to arrange for an accurate measurement of the temporal relations of the stimuli in this case. In case of the second series the finger was moved back and forth before the opening for an interval of not less than a second before the electric stimulus was given.

These experiments yielded results which were surprising in view of the previous work. *When the stimuli were given almost simultaneously the visual reinforced the electric, i. e., shortened the time of reaction.* As appears in the upper part of Table III, the average time of 40 reactions (20 for each frog) to the electric stimulus was 148 σ , and to the electric when it followed upon the visual, 128 σ . Furthermore, an examination of the pairs of reactions shows, as the table indicates, that there were 27 cases in which the visual stimulus caused reinforcement to 13 in which it caused inhibition. *When the visual stimulus preceded the electric by a considerable interval (1 second, see the right side of the table) exactly the reverse effect appeared, there was marked inhibition of reaction.* The averages are 150 σ for electric stimulation alone, and 178 σ when it was preceded by the visual stimulus. In this series there were 25 cases of inhibition to 14 of reinforcement.

TABLE III.

Reaction-time to Electric Stimulation Alone, and to the Same when Preceded for 0.1, 0.5 or 1.0 Second by Visual Stimulus.

Frog.	Electric Alone.	Visual 0.1'' before elect.	Number Inhibited.	Number Reinforced.	Number Equal.	Electric Alone.	Visual 1.0'' before elect.	Number Inhibited.	Number Reinforced.	Number Equal.
Preliminary Series. Visual Stimulus Moving Finger. Averages for 20 reactions.										
No. 5.	179+	158-	6	14	0	163	206-	14	6	0
No. 6.	116	98	7	13	0	136+	150	11	8	1
Gen. Aver.	148	128-	13	27	0	150-	178-	25	14	1
Visual Stimulus Moving Red Disc.										
Visual 0.1'' before electric.					Visual 0.5'' before electric.					
Series I. Averages for 25 reactions.										
No. 5.	177+	163-	10	15	0	170+	255-	15	9	1
No. 6.	148+	112+	6	19	0	115-	178-	18	7	0
Series II. Averages for 25 reactions.										
No. 5.	135+	120+	7	18	0	155+	259+	24	1	0
No. 6.	128-	111-	6	19	0	132+	227+	17	7	1
Gen. Aver.	147	126	29	71	0	143	230	74	24	2

In Table IV I have given the probable errors, standard deviations and coefficients of variation of the means, except in case of Series II.

4. Electric Stimulation and Moving Red Disc.

The indications of the importance of the temporal relations of stimuli, so far as reaction-time results are concerned, furnished by these crude preliminary observations led me to undertake a more accurate study of the subject. To this end a revolving disc, which moved at the rate of one revolution per

minute, was so arranged that at a certain point it closed an electric circuit in which I had placed a magnet. This magnet attracted a steel arm at the end of which a disc of red card-board 12 mm. in diameter was suspended. With the making of the circuit the steel arm was drawn downward suddenly and the red disc, by reason of the vibrations of the arm moved rapidly back and forth in front of a window in the reaction-box. In this way the moving object was exposed to view about 10 cm. to the right and 3 cm. in front of the right eye of the frog. The revolving disc, a fraction of a second later, completed the electric stimulus circuit. Thus both stimuli were given automatically, at such an interval apart as the experimenter desired. In the two series of results now to be described the intervals were 0.1 and 0.5 second respectively.

These series consisted of 25 pairs of reactions each, with two animals. The results of the series are presented separately because the experiments which constitute them were separated by a period of three weeks, during which time the conditions of the frogs changed noticeably; they became less active and less sensitive to stimuli.

The lower half of Table III contains a simple statement of the results of these series. It is to be noted that these results agree fully with those of the preliminary series. *The visual stimulus of a moving red disc, given 0.1 second before a 2 cell electric stimulus, reinforces the electric reaction, i. e., it shortens the time of reaction. The same visual stimulus given 0.5 seconds before tends to inhibit the electric reaction, i. e., it lengthens the time of reaction.*

Table IV contains the various values determined for the results of these series. The general averages for the results of the Preliminary Series and those of Series I are as follows:

Stimulus.	Mean, with Probable Error.	Standard Deviation, with Probable Error.	Coefficient of Variation
Elect. Alone. 180 reactions.	150.5 ± 5.48.6	38.55 ± 4.09.6	25.68
Elect. with Visual 0.1'' before. 90 reactions.	133.0 ± 4.93.	34.32 ± 3.23	26.84
Elect. with Visual 0.5'' or 1.0'' before. 90 reactions.	197.0 ± 14.19.	101.44 ± 10.03	50.74

Concerning the statistical values given in connection with this work certain important facts should be noted. First, the reactions are very variable. In fact the variability is so large that, were it not for the analysis of the pairs of reactions, the results could not be presented as conclusive evidence of the inhibitory or reinforcing influence of stimuli. But the fact that two times in three a visual stimulus almost simultaneous with electric stimulation of the skin shortens the time of reaction to the latter, whereas the same visual stimulus when given half a second before the electric lengthens the reaction-time in at least two-thirds of the cases, justifies us in putting confidence in the averages of the series despite the large probable errors and coefficients of variation.

The standard deviation of the electric reaction-time is unusually large because, in averaging, no selection was made from among the results. The apparatus was such as to permit reflex reactions, and as some of these (40 σ to 70 σ) are included in the series, as well as delayed reactions, the range is often from 40 σ to 500 σ. Arbitrary selection of reactions by limitation of the range did not seem advisable, and I have therefore presented the results as they were taken. Indeed, when we work with voluntary modifiable reactions, instead of with those that are forced, we must not expect either small errors or small variabilities.

TABLE IV.
Reaction-time to Electric Stimulation Alone, and to the Same when
Preceded by a Visual Stimulus.

Electric Stimulus Alone.				Electric Stimulus when Preceded for a Short Interval (0.1'') by Visual Stimulus of Moving Finger.		
Frog.	Mean. ¹	Standard Deviation.	Coeffi- cient of Var- iation.	Mean,	Standard Deviation.	Coeffi- cient Varia- tion.
No. 5.	179 ± 6.95 σ	46.09 ± 4.92 σ	25.75	158 ± 6.82 σ	45.21 ± 4.82 σ	28.61
No. 6.	116 ± 4.49	29.75 ± 3.18	25.65	98 ± 5.07	33.57 ± 3.58	34.26
Electric Stimulus Alone.				Electric Stimulus when Preceded for a Long Interval (1.0'') by Visual Stimulus of Moving Finger		
No. 5.	163 ± 4.17	27.66 ± 2.95	16.97	206 ± 9.29	61.54 ± 6.57	29.87
No. 6.	136 ± 5.71	37.88 ± 4.04	27.85	150 ± 9.66	64.02 ± 6.83	42.68
Series I. Electric Stimulus Alone.				Visual Stimulus of Moving Red Disc 0.1'' Before Electric Stimulus		
No. 5.	177 ± 4.74	35.12 ± 3.35	14.19	163 ± 3.57	26.45 ± 2.52	16.23
No. 6.	148 ± 6.37	47.25 ± 4.51	31.92	112 ± 4.27	31.65 ± 2.02	28.26
Series I. Electric Stimulus Alone.				Visual Stimulus of Moving Red Disc 0.5'' Before Electric Stimulus		
No. 5.	170 ± 5.05	37.45 ± 5.29	22.03	255 ± 21.47	159.21 ± 15.19	62.43
No. 6.	115 ± 6.37	47.25 ± 4.51	41.09	178 ± 16.34	121.09 ± 11.54	67.97
Average of all.				General Ave. of all 0.1'' Interval.		
	150.5 ± 5.48 σ	38.55 ± 4.09 σ	25.68	133 ± 4.93 σ	34.22 ± 3.23 σ	26.84
				Gen. Ave. of all .5 and 1'' Interval.		
				197 ± 14.19	101.46 ± 10.03	50.74

¹ Values were determined by use of the following formulae :

$$\text{Mean} = \frac{\sum (v. f)}{n} \quad \text{Probable Error of Mean} = \pm .6745 \sqrt{\frac{\sigma}{n}}$$

$$\text{Standard Deviation} = \sqrt{\frac{\sum (x^2. f)}{n}} \quad \text{Coefficient of Variation} = \frac{\sigma}{\text{Mean}} \times 100$$

$$\text{Probable Error of S. D.} = \pm .6745 \sqrt{\frac{\sigma}{2n}} \quad \sigma = \text{S. D.}$$

² Probable Error.

The fact that the variability of the reaction-time to an electric stimulus in connection with a nearly simultaneous visual stimulus is slightly less than that for the electric reaction-time is worthy of note, but it must be admitted that the difference is not sufficiently large to justify us in laying much stress upon the fact until further work furnishes additional evidence on the point. Clearly enough the greater variability when the visual stimulus precedes the electric by an interval of 0.5" to 1.0" is due to the increase in the number of delayed reactions, which in turn we may suppose to be the result of the visual stimulus. For these reactions, moreover, the range is greater than for the electric reaction-time, and a graphic representation of the distribution of the results shows that the mode is much nearer the 500 σ extreme than in case of the simultaneous stimuli series.

So far as my observations go (and it must be remembered that this research deals primarily with voluntary reactions) the statements thus far made concerning the influence of visual stimuli upon electric reaction-time hold for reflex reactions (by which is meant reactions in from 40 σ to 70 σ) as well as for the slower more deliberate reactions. If further investigation should confirm the suggestion which my results furnish it would lend additional support to work already done on the nature of the reflex; for MERZBACHER, not to mention the results of several other investigators, found that visual stimulation of the eye of the frog with a colored paper screen increases the extent of the reflex in response to cutaneous stimulation, or in other words, causes reinforcement of the reaction ('00, p. 250). As he has not studied the phenomenon with reference to the temporal relations of the stimuli, no comparison of his results with those of this paper are possible.

The literature of inhibition and reinforcement consists almost entirely of papers on the reflexes of animals, or on the volitional process of man, and in no instance have I been able to find any accurate statements concerning the significance of the temporal relations of the stimuli. WUNDT ('03, III, p. 443) states, as his belief, that the interference of unlike stimuli is greater than that of stimuli of the same qual-

ity. One sound delays the time of reaction to another, according to his findings, 45^σ, while a visual stimulus causes a delay of 78^σ in the auditory reaction. Apparently, in the researches thus far made, complication of stimuli more commonly causes inhibition than reinforcement. In the light of the results which have been considered in this paper it is of interest to inquire whether this may not be due to the fact that the temporal relation has not been considered. Possibly any two stimuli may be given in such relation that they will now inhibit, now reinforce one another.

An investigation by BOWDITCH and WARREN ('90) is of special interest in this connection, since they studied the influence on knee-jerk of various stimuli, given at different intervals with respect to the tendon blow. As appears from the following summary statement (p. 60-61) of their results there is striking agreement between their findings for this reflex and mine for the frog:

“(1) In the majority of individuals experimented upon a voluntary muscular contraction occurring simultaneously with the blow upon the knee increases the extent of the knee-jerk, but with the prolongation of the interval between the reinforcement signal and the blow this effect is reversed; the knee-jerk becomes much reduced in extent and may even entirely disappear. With a still further prolongation of the interval the knee-jerk gradually returns to its normal value. The interval at which the effect changes from positive to negative varies with different individuals from 0.22'' to 0.6''. The interval at which the knee-jerk returns to its normal value is 1.7''-2.5''. In two individuals the effect of muscular contraction on the extent of the knee-jerk was wholly positive.

“(2) The effect of a sudden auditory stimulus on the extent of the knee-jerk was, in the three subjects of experiment, almost wholly positive, though great individual differences were observed. The maximum effect was produced when the interval between the sound and the blow was 0.2''-0.3''.

“(3) The effect of a sudden visual stimulus upon the extent of the knee-jerk was with two of the three subjects of ex-

periment almost wholly positive, the maximum being reached when the interval between the flash and the blow was 0.1"-0.3". With the third individual a positive phase having its maximum when the interval was zero gave place rapidly to a negative phase reaching its maximum at 0.4"-0.8".

"(4) The effect of a sudden stimulus of the conjunctiva by an air blast was in general similar to that of a visual stimulus, except that the positive phase in all three individuals reached its maximum when the interval between the blast and the blow was 0.1", and the negative phase in the individual who manifested this phenomenon had its maximum at 0.8"-1.0"."

The effects of sudden stimulation of the nasal mucous membrane with a blast of air and of stimulation of the skin of the neck were very similar to those stated.

SUMMARY AND CONCLUSIONS.

1. Increase in light intensity from 1" to 2" before electric stimulation of the skin of the frog causes delay of reaction to the latter stimulus. If the electric stimulus be intense the inhibitory influence, as indicated by the time of reaction, is slight, if it be weak the inhibition is marked, and reaction may fail entirely.

2. Auditory stimuli give contradictory results. Sometimes they appear to inhibit, sometimes reinforce, the electric reaction. In case of the sound of an electric bell introduced (a) 0.1" before the electric stimulus, and (b) 1.0" before, the average for 300 reaction-times indicate a slight inhibitory influence.

3. Visual stimuli either inhibit or reinforce electric reactions according to the temporal relation of the two stimuli. (a) The visual stimulation of a moving object when given 0.1" before electric stimulation of the skin causes reinforcement of the reaction, i. e., shortens the reaction-time. (b) When given 0.5" or 1.0" before the electric stimulus the same visual stimulus causes inhibition, i. e., lengthens the reaction-time.

4. The experiments described prove that it is of import-

ance to consider the temporal relation of stimuli in any study of the relations of complexes of stimuli to sensory or motor processes. To say that two stimuli were given "nearly simultaneously" or "within a short interval of one another" does not suffice, for this unmeasured interval may make all the difference between the conditions necessary for reinforcement and those for inhibition.

5. If the meaning of the above statements in terms of the neural processes is demanded, only a speculative reply can as yet be given. Of theories of inhibition there are already enough; what we need is methods by which the neural process may be studied. Until we have more definite knowledge of what occurs in the organism in case of the mutual interference or reinforcement of stimuli it may be well for us to experiment much and speculate little.

A clear statement of what the neural changes which condition inhibition and reinforcement *may be* is to be found in a recent article on inhibition by McDougall ('03). So far as this paper is concerned it matters little whether inhibition be "assimilation," "drainage," "competition," or something yet unnamed.

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ON THE BEHAVIOR AND REACTIONS OF LIMULUS IN EARLY STAGES OF ITS DEVELOPMENT.¹

By RAYMOND PEARL.

Introduction.

In morphological research two modes of procedure are usually followed in investigating the significance of some particular structure of an organism. First the form, position, relations and other characteristics of the structure in the adult organism are studied. Then the embryological history is worked out for the purpose of ascertaining how the structure develops to the complex condition of the adult. In this way, of course, has been gained the complete explanation of many organs and structures which were inexplicable when the adult condition alone was considered. Indeed, embryological study has come to be considered an absolutely necessary part of almost any morphological investigation which aims at completeness. The ontogenetic history of an organ is regarded as of prime importance in elucidating the adult condition.

It is evident that the same thing may be true when the problem under consideration is one in animal behavior, instead of in animal morphology. As we go up the scale from the lower to higher forms, the behavior becomes more and more complex, and less easily resolvable into simple component factors. To be sure, the increase in physiological complexity does not run exactly parallel to the increase in morphological complexity, yet one does not have to go far before the analysis of the behavior of the adult organism becomes extremely diffi-

¹ Contributions from the Zoological Laboratory of the University of Michigan, Ann Arbor, Mich., No. 71.

cult of accomplishment. For some time before the present piece of work was begun it was the opinion of the writer that valuable aid in the analysis of the behavior of higher organisms might be gained by following the plan of the morphologist and studying the development in the individual of the characteristic features of the behavior. Just as the morphologist studies the ontogeny of an organ as an aid to the understanding of the adult condition, so might the comparative psychologist study the ontogeny of a reaction. It seemed reasonable to suppose, in view of the close relationship which JENNINGS and others have shown to exist between structure and type of behavior in lower forms, that in higher forms the behavior would be simpler in character during embryonic or larval life when the structure is simpler. Of course we know in a general way that this is true; but does it hold in detail for single complex reactions and reflexes? So far as is known to the writer, very little systematic work on behavior has been done from this point of view, except on some of the mammals and birds (cf. notably the work of MILLS, LLOYD MORGAN and SMALL). In these forms the behavior has evidently a considerable psychical element in it. It was with the idea of determining whether anything of importance might be gained by studying the ontogeny of reactions primarily reflex in nature that the present piece of work was undertaken.

The form chosen for study was the king-crab *Limulus polyphemus*. The reasons for this choice were two-fold; in the first place, I was already familiar with the behavior and reactions of the adult organism, and in the second place, *Limulus* is a form in which the behavior is quite complex, and yet at the same time the different reflexes are strikingly definite and machine-like in character. The adult *Limulus* is an almost ideal form for physiological work, on account of its tenacity to life after most extensive operations have been performed upon it, and because of the definiteness of its responses. Something of the complexity as well as the definiteness of its behavior can be gathered from the excellent account which PATTEN ('93) has given of the gustatory reflexes, for example.

The behavior of the adult *Limulus* is principally made up of the following movements and reflexes: the respiratory movements of the abdominal appendages, the swimming movements of the abdominal and thoracic appendages, various "gill cleaning" reflexes of the abdominal appendages and the sixth legs, walking movements, and the reflexes of gustation and deglutition. Furthermore, it responds to temperature stimuli very strongly and characteristically, also to certain sorts of tactile stimuli, to disturbances of its equilibrium, to chemical stimuli, and is thigmotactic and phototactic. The original plan of the present work was to make a thorough detailed study of the behavior and reactions during every stage of development from the time the embryo left the egg membranes till it attained the adult condition, in its behavior at least. It was hoped that in this way steps in the development of the reactions and reflexes could be traced.

The work was begun in the U. S. Fish Commission Laboratory at Wood's Hole, in July, 1900, and continued throughout the summer. In that time the behavior was studied and the work finished from my point of view (with the exception of the phototactic reaction) up to the stage at which the first moult occurs (end of the so-called "trilobite" stage). During the following fall a preliminary statement of the results obtained was published in *Science*.¹ It was expected at that time that the work would be taken up again the next summer and older stages studied. This, however, proved to be impossible and at no time since have I been able to take up the work again. As it is uncertain when I shall be able to go on with this problem it has seemed desirable to publish the results so far obtained. I wish to put on record the complete statement of the facts made out in the two developmental stages which have so far been investigated.

It gives me pleasure to make acknowledgement at this point to those who have in one way or another aided in this work. To Professor WM. PATTEN, my friend and former

¹ N. S. Vol. XII, No. 311, pp. 927-928, 1900.

teacher, I am indebted, not only for the material on which the work was done, which he very kindly furnished me, but also for many helpful suggestions freely offered as the work progressed. When the work on *Limulus* embryos was begun I had already been engaged for two years on a study of the physiology of the brain of the adult animal, under his direction. Without the thorough knowledge of the adult behavior thus gained the present study would hardly have been possible. To the authorities of the U. S. Fish Commission, and especially to Dr H. C. BUMPUS, I am indebted for the numerous facilities which were freely placed at my disposal at the Wood's Hole Laboratory.

Material and Methods.

The material used consisted of several hundred developing *Limulus* eggs which were given me by Dr. PATTEN. When received they were nearly all at about the stage of development, designated as Stage I, by KINGSLEY ('92). At room temperature development proceeds quite rapidly, but owing to the fact that there is a great deal of variation in the rate of development, individuals in widely different stages of development may be found at any time in the same batch of eggs. The eggs and embryos were kept in shallow glass dishes in sea-water which was changed at intervals, usually once in twenty-four hours. In this way the embryos were kept in good condition for a period of nearly two months.

The results of the present work will be discussed under two headings: first the behavior and reactions before the embryo leaves the egg membrane ("vicarious chorion," KINGSLEY's Stage I), and second, the behavior up to the time of the first moult after the animal begins its free existence (the so-called "trilobite" stage, KINGSLEY's Stage K). General accounts with figures of the morphological development of *Limulus* are given by KINGSLEY ('85 and '92).

The Behavior before the Embryo begins Its Free Existence.

Stage of Development.—The earliest stage at which definite results could be obtained regarding the movements and reac-

tions of the *Limulus* embryos was shortly before the time of hatching.¹ At this stage the embryo has a distinctly limuloid appearance in nearly all respects. All the appendages are formed, and are movable, with the exception of the long telson characteristic of the animal in later stages. The legs are formed on the same plan as those of the adult female, the secondary sexual modifications of the chelae of the first pair of walking legs in the male, not yet appearing. In this and the succeeding stages the embryos have a general, superficial resemblance to a trilobite which has led to the designation of these as the "trilobite stages" in the development. The embryo lies in the "vicarious chorion" (cf. PACKARD '72, and KINGSLEY, '85, p. 525) surrounded by fluid. The "vicarious chorion" is considerably greater in diameter than any dimension of the embryo, so that there is considerable free space on all sides of the latter. The embryo at this stage is about 4 mm. in length. The following account of the behavior within the "vicarious chorion" applies to embryos at any time within a week before hatching. Closer time relations than this, as will appear from the account, cannot be fixed in the development of the reactions of this organism.

Normal Position of the Embryo.—The embryo lies at the bottom of the hollow sphere formed by the "vicarious chorion," with its neural side uppermost. This position is simply the result of the action of gravitation, the embryo sinking to the bottom of the sphere because of the fact that its specific gravity is greater than that of the surrounding fluid. The reason for its lying with the neural surface uppermost is to be found in the fact (to be brought out in detail in another connection) that it is unable, under the circumstances in which it finds itself, to get into and retain any other position in which it is in stable equilibrium.

Movements within the "Vicarious Chorion."—In the descrip-

¹ I shall speak of the developing organisms throughout as "embryos." The rupturing of the "vicarious chorion" and beginning of free larval life, will be termed the "hatching." These expressions are used merely for verbal convenience.

tion of the movements of the embryo within the "vicarious chorion" the abdominal appendages will be considered first, as the phenomena here are relatively simple in character.

The abdominal appendages (operculum and gills) begin characteristic, rhythmical respiratory movements at least five days before hatching. It is probable that in reality such movements begin even earlier than this, but I have no observations going farther back. The ordinary respiratory movements when first observed are precisely like the same movements in the adult *Limulus*. They consist of a rhythmical, up-and-down beating of the gills, each gill book being opened during the phase of expansion, or "inspiratory" phase, to adopt the terminology of Miss HYDE ('94).

There is, however, one significant difference in the respiratory movements of embryos and adults. This is in the rate. In the adult the normal rate is about twenty-five to thirty beats per minute. In the embryos the rate is markedly more rapid, the average number of beats from my observations being sixty per minute. The range of variation is from 55 to 60 beats per minute. The rhythm of the beats is quite as perfect in the embryos as in the adults.

These respiratory movements are the only movements which the abdominal appendages perform before the embryo leaves the "vicarious chorion," so far as I have observed. I was never able to detect any tendency towards swimming movements of the gills before the time of hatching, although the embryos were under observation for six or more hours every day, and especial attention was paid to this point. This absence of swimming movements is rather remarkable in view of the fact that all the embryos begin swimming immediately after hatching.

In addition to the swimming movements the complex "gill-scraping" reflexes are absent, according to my observations, in embryos prior to the time of hatching. Certain of these reflexes have been described by Miss HYDE (l. c. p. 432, and Fig. 3). There also occur in adult *Limuli*, under certain conditions, complex gill-scraping movements of the sixth legs. I

have never seen these in the embryos before the time of hatching.

The intervals of rest in the respiratory movements, which in the adult occur frequently and may last for an hour at a time, are much less frequent in their occurrence in the embryos, and do not continue for such long periods.

For some time before hatching the thoracic appendages can be seen to be making active movements almost continuously. These movements vary greatly in force in different individuals, and at different times with the same individual. When they first appear they are usually very weak and increase in violence as development proceeds. At first it was thought that these movements were entirely random and aimless in character. They appeared to consist entirely of mere wavings and stretchings of the legs. Closer observation showed, however, that they were rather more definite than at first appeared. It was seen that they were the cause of the curious translatory movements of the egg as a whole. As the time of hatching approaches one notices very frequently that a particular egg lying by itself on the level, smooth bottom of a glass dish will suddenly begin to move, and slowly roll along the bottom, usually in a straight line. Frequently an egg will roll several centimeters in this way, although usually it does not cover more than from one to two centimeters.

These translatory movements of the egg as a whole are caused by the movements of the thoracic appendages in the following way. As the animal lies in the bottom of the "vicarious chorion," in the manner already described, the anterior and lateral margins of the cephalothorax are in fairly close contact with the inner surface of the "vicarious chorion." At this stage the chelae of the walking legs end in very sharp points. As a result of these two conditions, when the legs are extended the points of the chelae catch on the inside of the "vicarious chorion." The legs are usually directed somewhat forward when they are extended, and as a consequence of this and of the normal anatomical position of the legs it follows that the

chela catch at points lying on the anterior¹ hemisphere of the "vicarious chorion." Evidently then if the legs are extended, or in other words, the chela are strongly pushed away from the body, when they are caught in the "vicarious chorion," a movement of the embryo or of the "vicarious chorion" will be caused. Which of the two shall move, will depend on the circumstances. If the "vicarious chorion" is held in any way, the embryo is moved within it, in the following manner. The anterior edge of the cephalothorax is pushed more and more towards the lowest part of the hollow sphere in which the embryo lies, until finally the whole embryo is nearly or quite in a vertical position, resting on the anterior margin of the cephalothorax. If the legs still continue their kicking against the inside of the "vicarious chorion" the embryo is completely turned over and falls back to the lowest position of the sphere, with the haemal side uppermost.

On the other hand, if the "vicarious chorion" is not held in any way, the same action which in the previous case caused the embryo to turn over within it, causes the egg as a whole to roll slowly over the substrate. That this must be the case is evident if it is remembered that the weight of the embryo tends to maintain the latter in a constant position with reference to the center of the earth, while the hollow sphere, against the inside of which it is pushing, is rotated about it. On account of the fact that the embryo lies in a fluid in the "vicarious chorion" there is practically no internal friction to hinder this rotation of the sphere about it. It will be seen that, from the point of view of mechanics, whether the "vicarious chorion" as a whole shall rotate or not, depends on the relation which happens at the time to prevail between the weight of the embryo and the external forces hindering any movement of the sphere. If the weight of the embryo overbalances the external forces the sphere will rotate, while on the other hand, if the external

¹ Of course the terms anterior and posterior are here used to refer to the portions of the "vicarious chorion" nearest, at any given time, to the anterior and posterior ends of the embryo.

hindrances are great enough to overbalance the weight of the embryo, the latter will turn over within the sphere.

In the movements of translation of the eggs as a whole the direction of the movement is usually such as to keep the abdomen of the embryo in advance. This is a mechanically necessary result if the movements are produced in the manner just described. Of course, circumstances will sometimes prevent the egg from moving in a perfectly straight line, and again, the pressures exercised by the legs on the two sides of the body are not equal in amount. That they are about equal in the long run is shown by the fact that in the great majority of cases when free movement of the egg for some distance occurs, this movement is very approximately in a straight line. In cases where the movement is somewhat irregular the longitudinal axis of the embryo may not lie exactly in the path of motion, yet in no case have I ever seen the anterior end of the embryo in advance in the free translatory movements of the egg. The movements are always either somewhat sidewise with reference to the embryo, or, much more commonly, with the abdomen in advance.

In the behavior just described there is no definite co-ordination in the movements of the legs. Each leg acts by itself, and there is no rhythmic order in which the different legs move, as is the case, for example, in the gustatory reflexes of the adult *Limulus* (cf. PATTEN, '93, pp. 7-9).

The behavior when the "vicarious chorion" is held so that it cannot move offers some points of interest. The embryo is seemingly unable to maintain itself with the haemal side uppermost even after it attains that position in the manner described above. This is apparently a consequence of the fact that the organism after getting into the upright position does not stop the movements of the legs. When the legs are extended with the animal in an upright position the whole body is of course raised till its haemal surface is nearly in contact with the uppermost part of the sphere. When the embryo is in this position, if the effective pressure of the legs becomes greater on one side than on the other, as invariably happens, it forthwith

topples over and rolls down till it lies in the usual position in the bottom of the "vicarious chorion" with the haemal side up. I have seen this series of actions repeated time after time by the same embryo. It usually takes several minutes of strenuous labor for the embryo to get righted in the "vicarious chorion," and then within a few seconds of the time it attains that position, it suddenly loses its balance and falls back to the point from which it started. Then the same series of events begins again. There is nothing in the behavior which would in the least suggest any process of "learning by experience," or of perfecting a reaction by practice.

The stimulus which induces these almost continuous leg movements in the embryo is probably of the same sort as that which causes the righting reaction in the adult *Limulus*. If adult *Limuli* are placed in water so that the haemal side is in contact with the bottom, they immediately give a characteristic reaction which brings them into the normal position. From a long series of observations and experiments on the adult animals it appears that this apparent "equilibrium sense" is primarily due to a strong positive thigmotaxis of the neural surface of the body, together with a negative thigmotaxis of the haemal surface. A similar condition of affairs has been shown to be the cause of the righting reaction in other organisms (cf. PEARL, :03 for *Planaria*). It seems to me probable that the leg movements of the embryos when they are in an inverted position are thigmotactic responses. The only essential difference between embryo and adult in respect to this thigmotaxis would then be that the definite, purposeful reaction with which the adult meets and solves the difficulty has not yet developed in the embryo. Instead the embryonic thigmotactic reaction is simply a generalized response to a general stimulus. The reaction becomes specialized and better adapted to the accomplishment of its end as development proceeds.

The movements of the thoracic appendages which have been described are the only ones which I have observed before the time of hatching. None of the complex, coördinated re-

flexes of the legs, such as the gustatory and swimming movements, appear at this early stage.

Reactions to Stimuli.—It is rather surprising to find that before the time of hatching the embryos are extremely sensitive to mechanical stimuli applied to the external surface of the “vicarious chorion.” If the surface of the “vicarious chorion” be touched very gently with a needle the embryo stops all movement at once, draws the legs back as far as possible into cephalothorax and strongly flexes the abdomen, so as to make practically a right angle between it and cephalothorax. These positions are maintained as long as the stimulus is continued. In a short time after the stimulation ceases the abdomen is extended, and the respiratory and leg movements begin again.

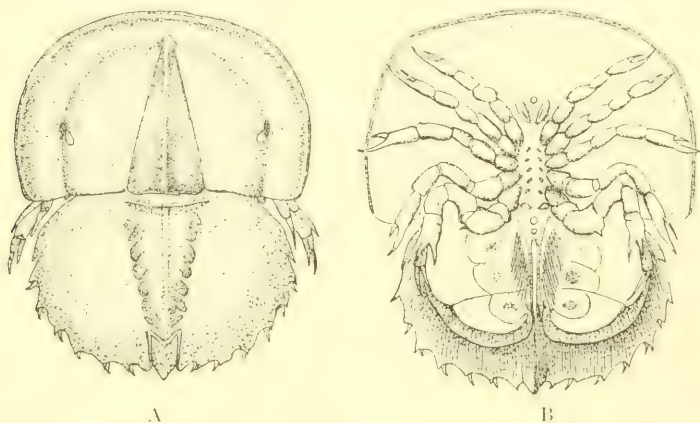


Fig. 1.—Diagrams showing appearance of *Limulus* embryo immediately after hatching. A. Haemal side. B. Neural side. (After KINGSLEY).

This is the same reaction as that given in response to mechanical stimuli after hatching. It is somewhat remarkable that the organism should respond in the same way to the pressure of a needle point when in one case this pressure has first to be transmitted by the surrounding fluid to the embryo, and in the other case the needle point touches the surface of the body directly.

Hatching.—The behavior at the time of leaving the “vicarious chorion” I have not been able to observe. In the material which I had all the hatching occurred during the night.

The Behavior after Hatching.

Appearance of the Organism.—In general form the embryo at this stage closely resembles the adult *Limulus* except for the absence of the elongated telson. The appearance of the embryo in dorsal and ventral aspects is shown in Fig. 1, A and B. This stage is KINGSLEY'S (loc. cit.) Stage K.

Movement of Abdominal Appendages; Respiratory Movements.—The respiratory movements continue after hatching in the same characteristic manner as has been described above for the preceding stage in development. The only difference in them is found in the rate, which becomes somewhat more rapid. According to my observations the rate of the beat after hatching stands in about the ratio of 5 to 4 to the rate while the embryo is within the "vicarious chorion." During some experiments in which the embryos were taken from the water and placed on moist sand, with the haemal side uppermost, it was observed in several cases that the respiratory movements continued in the normal manner, while the embryo was out of water. This was a rather unexpected finding, for the reason that adult *Limuli* never perform continued, normal rhythmical movements except in the water. The only explanation for the case of these young embryos which has suggested itself to me is that possibly at this stage of development the gills are less sensitive to changes in the surrounding medium than they are to the adult. This, however, does not seem very probable, in view of the fact that the general tactile sensitivity of the embryo at this stage is greatly in excess of that of the adult.

Swimming.—Immediately after the embryo leaves the "vicarious chorion" characteristic swimming movements begin. So far as the abdominal appendages are concerned these movements are precisely the same in embryo and adult. They consist of strong extensions and flexions of the gills¹ with reference to the abdomen. They are rhythmical, and are essentially

¹ Throughout the paper where statements are made concerning the performance of swimming movements by the "gills" it will be understood that the gill covers and the operculum are the organs to which reference is made. The term "gills" is used merely to avoid circumlocution.

like the respiratory movements except that the amplitude and force of the beats are much greater in the swimming than in the respiratory movements. On account of the fact that the gills are extended so as to form nearly a right angle with the body at the beginning of each beat a considerable portion of the effective force of the stroke is directed nearly straight backward.

There is a very marked and fundamental difference between the swimming movements of the embryo and the adult with respect to the thoracic appendages. In the adult *Limulus* all the walking legs beat strongly back and forth in time with the gills during the swimming. As the gills are raised the legs are extended and thrown far forward in the cephalothorax, and as the gills strike backwards the legs accompany them in this movement. In the embryo of the stage under discussion, however, the legs take no part whatever in the swimming movement. Whenever the gills begin swimming motions the legs are extended as much as possible and thrown forward until they touch the antero-lateral margins of the cephalothorax. Then they are held rigidly in this position as long as swimming continues. The appearance in swimming is as if the legs became temporarily paralyzed and held in a "forced" position while the gills were performing swimming movements.

A very interesting course of development is to be observed in connection with the ability of the embryo to direct its movements when swimming. The usual position of the embryo, if lying by itself in the dish, is the same as its position in the "vicarious chorion," namely, lying on the bottom in an inverted position. As has already been stated, swimming movements begin at once after the embryo is hatched. For some time after these movements begin, however, the embryo is not able to rise from the bottom. The gills beat most energetically, but the only result is to cause the embryo to slide along the smooth bottom of the dish. It has not acquired the faculty of so bending the abdomen with reference to the cephalothorax as to make the force of the swimming raise it from the bottom. That this failure to rise is not due to lack of power in the gill

strokes is certain, from evidence to be presented later. To such an extent is the organism unable to direct its movement in these early stages that, instead of tending to swim up from the bottom, it actually tends at times to swim downward. In many cases I have seen the beating of the gills become so forcible as to raise the abdomen and send the embryo skimming along the bottom on the antero-haemal surface of the cephalothorax. If, under these circumstances, the anterior margin of the cephalothorax happens to meet an obstacle in its path the embryo will in many cases turn completely over on its anterior end as a pivot, and come down with the haemal surface uppermost. The "summersault" in such cases is caused solely by the continued violent swimming movement of the gills while the anterior end is held.

How then does the embryo get up from the bottom at this stage, so as to swim freely through the water? This is done in one of two ways, during the earliest stages after hatching. The first of these methods is purely accidental so far as the organism is concerned. If an embryo which is sliding along the bottom as the result of the violent swimming movement of the gills happens to strike squarely a very small obstruction in its path, the anterior end of the body will in some cases slide up onto the obstruction. This, of course, gives the body as a whole an upward tilt and if the swimming movements continue the embryo will rise clear of the bottom and swim freely through the water. Sand grains and pieces of cast egg membranes usually serve as the means for starting the animals upward in this way. Rising in this manner only occurs infrequently, since it is not often that all the necessary conditions will be fulfilled together. After the embryo gets started in this way it is able to sustain itself in the water for as long as a minute even in very early stages of its free existence. Such cases show that the ordinary inability of the embryo to rise from the bottom is not due to lack of force in the swimming movements.

The second and more usual method by which very young embryos rise from the bottom is by first turning over from the usual position with the haemal side down, and then starting to

swim from the upright position. As will be described in detail later, the embryos are able under certain conditions to right themselves after hatching. It very frequently happens with the youngest embryos that an individual in the upright position (i. e., with the neural side down) will suddenly start violent swimming movements with the gills. When this happens the embryo immediately moves forward and upward away from the bottom. For a short distance (varying in different cases) it maintains the upright position while free in water, but in a very short time after starting in every case it topples over and falls into the normal position for swimming, that is with the haemal side down. It then continues swimming in quite the normal way.

As development proceeds the swimming becomes better controlled and the embryo gains the power of rising from the bottom by swimming without first turning over. The earliest stage at which I have seen embryos do this was about forty-eight hours after hatching. Even at this time the embryos do not rise directly from the bottom, but first slide along the bottom for a distance of from three to five centimeters and then gradually veer upward. In about a week after hatching the swimming is under perfect control in all cases. The animals rise at once from the bottom, and direct the movement quite as well as does the adult. Apparently the only difference between embryos of this stage and adults with respect to the swimming is in the fact that the legs remain quiet in the case of the embryo.

A problem in connection with the swimming movements in the embryo in which I was especially interested was this: Why is it that swimming movements of the gills appear immediately after hatching, while before that time no indication of such movements are to be observed? The most probable explanation seemed to be that the swimming was a purely reflex movement which needed the stimulus of the normal sea-water on the sense organs of the gills to set it into action. In other words, the reflex mechanism was complete in the embryo be-

fore hatching and swimming would have gone on there if the proper stimulus had been given.

In order to get further evidence on this hypothesis experiments were tried on hatched embryos, with a view of determining whether the chemical composition of the water influenced the swimming movements. Embryos were put in solutions of the following compositions:

A. Fresh sea-water 1 part

$\frac{n}{10}$ NaCl 1 "

B. Fresh sea-water 1 part

Rain water 1 "

The results so far as the swimming movements were concerned were essentially the same with the two solutions. There was practically no swimming in the concentrated sea-water, and very little in the diluted solution. Individuals would occasionally make spasmodic beginnings of swimming movements but these usually continued only for a few beats. The swimming movements were better in the diluted than in the concentrated sea-water, but in both series the total amount of swimming done was very greatly reduced in comparison with what goes on under normal conditions. Control series in normal sea-water demonstrated that these results could not be due to light or temperature effects. Other movements than swimming (walking, respiration, etc.) were not affected in solution B, and in solution A only after the experiments had continued for over 48 hours. The sensitiveness of the embryos to chemical stimulation was not apparently affected in either solution.

These experiments, so far as they go, give confirmation to the view that the necessary stimulus for the swimming reflex is afforded by normal sea-water. It was impossible, on account of lack of time, to absolutely prove that this is the case, but I think we are justified in concluding that there is a considerable degree of probability that this is the explanation of the fact that swimming movements do not occur while the embryo is within the "vicarious chorion," but begin immediately after hatching.

The proportionate amount of time spent by the embryos in swimming movements as compared with aimless leg movements or in walking movements, becomes progressively greater as development proceeds, during the "trilobite" stage. During the period immediately following hatching the embryos appear to become quickly exhausted by violent swimming movements. As development proceeds they get stronger until during the week immediately preceding the first moult after hatching nearly all the time is spent in swimming.

I have never seen in embryos at this stage any indication of the "forced" gill cleaning reflexes of the gills themselves which occur in the adult, and have been described by Miss HYDE (loc. cit.).

Movements of the Thoracic Appendages.—When the embryos are lying in an inverted position at the bottom the legs are practically continuously in motion. Immediately after hatching these movements are of the same character as those within the "vicarious chorion." The hatched embryo, however, has nothing for the chelae to engage and consequently the movements accomplish no purpose. These leg movements are probably still to be regarded as an incipient righting reaction (cf. above). Throughout the whole of the "trilobite" stage the embryos do not develop a definite, immediately purposive righting reaction like that of the adult. These young embryos right themselves in a great variety of ways and in nearly every case it is a long and tedious process. The most usual way is for one embryo to rather indefinitely push against or crawl over a second individual or a cast "shell" or some bit of debris in the water till it gets righted. The nearest approach to a definite righting reaction which I have seen in these very young individuals is a combination of swimming and leg movements. As has been described above violent swimming movements of the gills sometimes serve merely to raise the abdomen of an inverted embryo without causing the animal as a whole to rise from the bottom. This results in making the embryo practically "stand on its head" (i. e., rest on the extreme anterior margin of the cephalothorax). Not infrequently when

an embryo has reached this position it will suddenly release the legs from the cramped position into which they are thrown when the gill swimming begins, and start scratching with the chelae against the bottom in front of the anterior margin of the cephalothorax. The evident purpose in this act is to help out the gills at the critical moment, with the legs. The result usually is that the embryo immediately gets over into the normal upright position. This reaction is of interest as indicating the greater strength of the positive thigmotaxis of the chelae as compared with the tendency for the legs to be held in a forced position during the gill swimming. The tips of the chelae when the legs are in the forced position during the swimming project in front of the margin of the cephalothorax. When the posterior end of the embryo is raised far enough the chelae will evidently touch the bottom, and this stimulus is sufficiently strong to overbalance the tendency for the legs to hold the cramped position, and to cause them to kick against the bottom.

The stimulus which calls forth all these attempts of the embryo (the same is also true of the adult) to right itself, comes, I believe, primarily, from the strong positive thigmotaxis of the neural surface of the body, and especially of the margin of the cephalothorax and the tips of the chelae, together with a negative thigmotaxis of the haemal surface.

As the time of the moult which terminates the "trilobite" stage approaches a very definite and curious reaction of the thoracic appendages develops. In its typical form this reaction is as follows: let a needle, or any other object of similar size, be held parallel to the long axis of the body so that the ends of one or more of the chelae touch it in the course of their movements. Immediately all the legs will close over the needle and, in a way, hug it up to the body. At once the embryo begins to crawl along on the needle held in this way. Even if the needle is held so as to be perpendicular to the bottom of the dish the embryo will crawl up on it as far as the surface of the water, and even in some cases rise partly out of the water. So firm a grasp do the legs have on a smooth needle that with moderate care an individual may be raised entirely out of the

water by lifting the needle. This reaction cannot be induced immediately after hatching, and only reaches its greatest perfection towards the end of the "trilobite" stage. It is a very definite and striking piece of behavior and may be induced with perfect certainty at every trial in late "trilobite" embryos. It can apparently only be classified as a form of thigmotactic reaction, and seems to me to be significant chiefly in indicating the degree of coördination in leg movements which has developed since hatching. What, if any, significance such a reaction can have in the life of the embryo under the normal conditions of existence I am unable to conjecture. It seems to be merely a reaction very perfectly adapting the embryo to the business of climbing up slender sticks or needles, and, so far as I know, there are no natural demands in the normal existence of the animal at this stage of development which would make such a reaction either necessary or even useful. I observed this reaction as first occurring about one week prior to the time of the moult which ends the "trilobite" stage.

Walking Movements.—Immediately after hatching the walking movements are very irregular. There is apparently little coördination between the different legs, and as the animal progresses it rocks and sways from side to side and frequently falls over on one side. As development proceeds the movement becomes somewhat better coördinated. This form of locomotion is, however, even in the adult, a poorly coördinated one, the organism being much better adapted to swimming than walking. The embryos got on better when walking on a rough surface like the sand bottom, than on a smooth surface like glass.

Avoidance of Obstacles in the Path.—Neither when walking nor when swimming do embryos show any perception of an obstacle in the path before they strike it.

If a very young embryo when walking strikes an obstacle like a needle held in its way, no attempt is made to get around it. Instead, the embryo will continue to walk straight ahead pushing the anterior margin of the cephalothorax against the obstacle. This action will be continued till, by chance, in the

unsteady walking movements the body gets pointed in a new direction such that the obstacle no longer completely stops the progressive motion. Then, of course, the embryo is able to push around, and continue on its way. A large number of observations were made on this subject to determine whether older embryos developed any distinct purposeful reaction to enable them to get around obstacles. I was unable to convince myself that there was any real progressive development in this matter. Sometimes older embryos will stop walking when they strike an obstacle, fall back perhaps half the length of the body, and then start forward again in a path at an angle to the former line of motion. This will take them by the obstacle at once. This behavior, however, does not occur with sufficient frequency to warrant considering it a typical reaction. The typical behavior throughout the "trilobite" stage seems to be essentially that first described.

Burrowing Reaction.—If *Limulus* embryos in the "trilobite" stage are taken out of water and put on moist sand they will usually in a short time burrow into the sand so as to be completely buried. This behavior is of a character which would warrant it being characterized as instinctive. Analysis shows, however, that it is capable of explanation in another way. When an embryo is placed on the sand it starts walking in the usual way. This continues until some obstacle in the path stops further movement ahead. Then, as has been described in the preceding section, the animal pushes against the obstacle. Now when this action takes place on sand the sand grains are pushed out from below the embryo as a result of the action of the legs. The violent movements of the legs tend to raise the abdomen, and the anterior end gets pointed more and more down into the sand. As walking movements of the legs continue more and more sand is thrust from below the animal, and the whole body is thrust downward and forward. In this way the burrowing is brought about. Any sort of obstacle in the path will induce the burrowing when the embryo is on sand, so far as I have observed. A needle held in front of the animal

will start the burrowing; a small pebble or a few projecting sand grains in the path produce the same result.

The burrowing reaction is then evidently started primarily as a result of the strong positive thigmotaxis of the margin of the cephalothorax. This thigmotactic tendency is so pronounced that the mere catching of the anterior margin of the cephalothorax on a few sand grains is sufficient to start the animal pushing ahead into the sand. I have frequently seen the burrowing started in this way.

The reflex nature of the burrowing reaction is well shown in some cases I have observed in which an embryo which had started burrowing and had succeeded in burying perhaps half the body, would, by the violence and lack of good coördination of the leg movements, accidentally lift the anterior end out the hole which it had excavated. Such individuals, in every case observed, did not return to the burrowing but walked off over the sand in whatever direction they were pointed, until they chanced again to get the anterior margin of the margin of the body caught by some obstruction.

Complex Reflexes.—During the stage of development under consideration the "gill scraping" reflexes of the sixth legs appear. These consist in complete extensions and flexions of the sixth legs with the surface of the abdominal appendages. The reflex is a very characteristic one and its apparent purpose is to free the outer surface of the gills of any material which might prove injurious. These movements appear at once in their perfect form, so far as I have been able to observe. There is no process of gradual perfection by practice, or learning. The action is performed for the first time by the embryo in quite the same manner that it is by the adult.

Reactions to Stimuli.—The reaction of embryos in the "tribolite" stage to tactile stimuli of all but the weakest intensities is precisely the same as that described above for the preceding stage. It consists in a strong contraction of all the flexor muscles of the body. This state of contraction persists as long as stimulation is continued. There are no differentiated responses to localized tactile stimuli. The same effect is produced what-

ever part of the body is stimulated. The reactions to very weak tactile stimuli applied to the tips of the chelae have been described above (p. 155).

The characteristic gustatory reflexes of the adult *Limulus* (cf. PATTEN, '93) I have not been able to induce in embryos of the "trilobite" stage. Repeated experiments were made on this point with the substances which produced prompt and strong chewing movements in the adult, but always with negative results. No distinct reactions of the legs are produced when clam juice is dropped on the coxal joints. The absence of these reflexes is probably correlated with non-development of the sense organs which are stimulated by edible substances.

The adult animal is very sensitive to weak thermal stimuli, responding promptly and in a characteristic way to a puff of warm air, or to the warmth of the hand laid on the margin of the carapace (cf. PATTEN, '93). The embryos fail to show this sensitiveness to thermal stimulation. They will only respond to a strong temperature stimulus such as is given by holding a red-hot needle very close to the body, and then the reaction is a general one, like that given in response to tactile stimulation. The absence of characteristic temperature reflexes is again probably to be explained as due to the non-development of the proper sense organs at this stage.

Several years ago LOEB ('93) gave a brief account of the reactions of *Limulus* embryos in the "trilobite" stage to light. The essential results of this author's work are given in the following sentences (loc. cit., pp. 98-99). (1) "Die Larven von *Limulus polyphemus* sind nach dem ausschlüpfen auf dem Ei positiv, später negativ heliotropisch." (2) "Die positiv heliotropischen Bewegungen werden stets schwimmend, die negativ heliotropischen stets kriechend ausgeführt." Throughout the course of the present work considerable attention was paid to the subject of phototaxis, and a large number of experiments along this line were performed. It very soon appeared that there were other factors present in the reactions to light, besides those enumerated by LOEB. The case is not by any means as simple as his account would indicate. The conditions

under which the present work was done made it practically impossible to carry out a thorough and complete investigation of the phototaxis of the embryos, so that in several particulars my results are incomplete. For this reason it seems preferable not to publish my observations in detail at this time. For the sake of indicating the general trend of the results as far as they go I will briefly summarize them. I was unable to get any evidence that the first reaction to light to appear after hatching was positive in sense. On the contrary it was clearly negative, regardless of whether the embryos were swimming or walking. Later there appeared a strongly marked positive reaction shown only by relatively few individuals. These individuals when responding in the positive sense to the direction of the incident light were, so far as my observations went, always swimming in a very violent manner. In the same dish at the same time, with all the embryos of approximately the same age, many individuals were negatively phototactic, fewer positively phototactic, and still fewer apparently indifferent to light. This applies to light of the intensity of diffuse sunlight. The negative phototaxis is apparently associated with a strong positive thigmotactic tendency.

It seems very desirable that the reactions of *Limulus* to photic stimuli in any or all stages of its development be thoroughly investigated under proper conditions for experimentation. I know of no form which seems likely to give more interesting and significant results in this field than this organism.

Discussion of Results.

With the detailed results now in hand it is possible to make a direct comparison between the behavior of *Limulus* in its earliest larval stages and in the adult condition. In order make the comparison easy of comprehension the following table has been arranged. In parallel columns are stated the conditions with respect to certain definite features of the behavior in the two stages of the life history.

Tabular Résumé of the Behavior of *Limulus* in the Earliest Stage of its Free Existence, and in the Adult.

	Embryo.	Adult.
<i>Respiratory Movements.</i>	Same in character in embryo and adult.	
<i>Swimming Movements.</i>	Gills only beat rhythmically. Legs held in fixed position. Gill movements the same in character as in the adult. Control of swimming movement poor immediately after hatching. Improve with practice.	Legs and gills both beat rhythmically and synchronously.
<i>Walking Movements.</i>	Essentially the same in character in embryo and adult. Not so well coördinated and directed in embryo as in adult. Improve with practice in embryo.	
<i>Righting Reaction.</i>	Present from beginning but not well coördinated. Not as definite in type as in adult.	Definite, immediately purposive reaction.
<i>Burrowing Reactions.</i>	Probably same in embryo and adult.	
<i>Gustatory Reflexes.</i>	Absent.	Complex and highly coördinated.
<i>Temperature Reflexes.</i>	Absent.	Definite and purposeful reflexes.
<i>"Gill-scraping Reflexes of Sixth Legs."</i>	Essentially the same in embryo and adult.	
<i>"Cleaning" Movements of Gills.</i>	Absent.	Present (cf. HYDE, loc. cit.)

From this comparison it appears at once that, with a single exception, all the items of behavior presented by the adult are, in the case of the embryo, either entirely absent or present in essentially the same condition as in the adult. In other words, the embryo does not in general have simple types of be-

havior, which during development give way to more complex types leading up to the condition found in the adult. This seems to be a matter of some importance, for the reason that it indicates that it will be nearly or quite useless to look to larval stages for help in analyzing the adult behavior in forms like *Limulus*. It seems likely from what we know of the general correlation between type of behavior and general type of body form, that the same thing will be true in most cases where the general form relations of the body are closely similar in larval and adult stages. In *Limulus* this similarity in body form is very close, and the present paper shows how similar in essential features the behavior is in the two stages.

The single exception to the general rule of essential similarity in type of behavior between adult and embryo in *Limulus*, is found in the swimming movement. In the embryo the legs take no active part in this movement, while in the adult they beat synchronously with the gills. So far as the legs are concerned we evidently have here a simpler type of behavior in the embryo than in the adult. The holding of the legs in a cramped position as described must be regarded as a definite action, just as any movement would be, only it is simpler in character than a rhythmical movement. The difference here in behavior between embryo and adult is without doubt associated with a morphological difference in the nervous mechanism.

In the case of swimming and walking movements, and the righting reaction the study of the embryos give indubitable evidence that there is improvement with practice. The embryo performs these movements better—that is, with steadily increasing purposiveness—the more it practices them. At the time of hatching it is endowed, so to speak, with an ability to perform certain acts, but is unable to perform them in such a way that they serve any purpose at all well. The latter ability comes with practice. Shall we call this “learning through experience” how to do certain things? It seems to the writer that one who maintains that it should be so called will occupy a practically impregnable position, yet he will be totally unable to prove that this necessarily involves any psychical element.

On the other hand, the phenomena in a case like the one under discussion appear objectively analogous to certain phenomena in the inorganic world. For example: one gets a complicated piece of machinery fresh from the factory. If energy is put into it it will do certain things. But on account of the newness the parts do not work smoothly together. There is an undue amount of friction between the parts. As the machine is used the bearings get worn a little and we say that as a whole the machine "works better." The continued functioning improves the general coördination as a result of the interaction of the parts. Objectively very much the same *sort* of change appears to take place in the behavior of a *Limulus* embryo. Is there any more of a psychical element in the one case than in the other? This we obviously do not know, and it seems idle to discuss the question, since no amount of *a priori* reasoning will settle it and *a posteriori* evidence is not to be had.

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EDITORIAL.

Since the days of GERLACH's reticulum there has been a growing tendency among neurologists of all schools to lay great stress on the functional importance of the neuropil, or felt-work of finest non-medullated nerve terminations. It would appear that here some of the most characteristic nervous reactions take place, and that the peripheral fibrillar networks are not less important. Just what these reactions are it is still too early to affirm with confidence, but the problem is being attacked from several sides and with a fair prospect of immediate success in some of its phases.

Anatomical interest centers now on neurofibrillae and enough facts have already been gathered in to justify the prediction that we shall not have to wait much longer for an accurate knowledge of what the structure of the neuropil really is. Physiological experimentation, too, is daily adding new facts and developing new points of view. Undoubtedly both of these classes of evidence must be greatly enlarged before we shall be in a position to determine just how far the newer conceptions of nervous function can be cast in the mold given by the terminology of the neurone as current in the decade just closed. Certain it is that we are not yet ready to throw away that terminology; for even a contracted and defective mold is better than none so long as it turns out fruitful hypotheses and promotes clear analysis and accurate expression, provided only one does not make a fetish of it and in the end perhaps come to venerate its very defects. Practically, even the most striking of our latest physiological experiments on the functional differentiation of the nervous elements can still be expressed more conveniently in terms of the neurone doctrine than in any other way.

This much, at least, is clear, that the nervous system is not made up of structural elements (neurones) in the same sense that a house is built up of bricks or even that the liver is made of cells. The functional unit of the nervous system is the conduction path or functional system of neurones, and for aught that we know to the contrary, the same neurone may be a member now of one functional circuit, now of another totally different. This is suggested, not only by the familiar anatomical connections of the associational centers and simpler reflex stations of the brain, but also by some more recondite phenomena, such as the vicarious functioning of one cortical area after injury to another.

Still more striking in this connection are the cases of substitution of function after peripheral nerve anastomosis, such as that recorded by CUSHING and referred to in our last issue. After traumatic destruction of the facialis root and resultant paralysis, the central end of the spinal accessory nerve was sutured on to the peripheral facialis and a successful union effected. There resulted total permanent paralysis of the trapezius and sterno-mastoid muscles and almost perfect restoration of facial symmetry both at rest and (less perfectly) in the facial movements.

Experimental cross-suturing has long been practiced on lower animals and LANGLEY has recently been reporting in the *Journal of Physiology* a series of such operations, especially upon the cervical sympathetic. In a case reported upon in February of this year the fifth cervical nerve in a kitten was sutured to the cervical sympathetic and functional union resulted. After 187 days, stimulation of the fifth cervical nerve caused the usual effects produced by stimulation of the cervical sympathetic. Since the fifth cervical root contains no pre-ganglionic sympathetic fibers it follows that "certain somatic nerve fibers are capable in favorable circumstances of making functional connection with sympathetic nerve cells."

It is evident that such remarkable changes in peripheral connections must result in profound changes in the central conduction pathways, and that too probably without the loss of

any central neurones. This plasticity of the central organ, then, seems to be functional largely, not merely regenerative or structural. And this again will have an application in any attempt to define the value of the neurone.

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Some progress has been made with the functional analysis of the neurone. VAN GEHUCHTEN'S law of the polarization of the neurone (the dendrite being cellulipetal, the neurite cellulifugal), while certainly not universally applicable, is nevertheless quite generally true in higher vertebrates. The selective action of certain drugs on parts of the neurone is well known. Thus, curare will paralyze the terminal arborization (motor end-plate) of peripheral somatic motor neurones without destroying the functional integrity of the remainder of the neurone, and it is probable that nicotine acts in a similar way upon the terminal arborization of the pre-ganglionic sympathetic neurones. And, still more recently, LANGLEY has made it very probable that the difference between vaso-constrictor nerves and vaso-dilator nerves lies in the mode of the ending upon the unstriated muscle cells of the arteries of the post-ganglionic sympathetic neurones involved, and not upon the general character of these neurones or their central connections.

Of much greater importance is the differentiation within the neurone of neurofibrils and a more fluid plasma—apparently a conducting substance and its nutrient stroma. And the further differentiation within the latter of NISSL bodies, we are taught, is a device for the distribution of a modified nuclear chromatin to facilitate rapid metabolism in the cytoplasm.

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We hear much recently about neo-vitalism in biology. In the minds of some the mechanical theory of life is on the decline. It is asserted that physics and chemistry have not explained organic phenomena as was anticipated by the defenders of the mechanical theory fifty years ago. Many biological facts are not as yet capable of satisfactory explanation in terms of

any known physical or chemical laws. To ask whether, when we have arrived at a complete knowledge of the organic world, the biological phenomena will be found to be explicable in terms of the laws of the inanimate world, is to miss the true significance of the problem. The truth is that both vitalism and the mechanical theory are undergoing transformation. Each is being interpreted in terms of the other. The reason that the mechanical theory today is inadequate to explain all the biological facts is that this theory was formulated upon the basis of too narrow a range of phenomena. If it is to remain the working hypothesis of the physiologist it must be allowed that development which, as itself an organic phenomenon, every working hypothesis exhibits. To take the mechanical theory as a rigid concept, as it was fixed by thought half a century ago, is logically as vicious as to push recklessly forward to an unwarranted vitalism. In so far as the neo-vitalism is a protest against the static character of this mechanical theory, it may well be that the truth lies, for the time being, in this swing of the pendulum towards vitalism. It behooves the defenders of the mechanical theory to look to the vitality of the mechanical theory itself.



There are no neurological researches which American students can claim as their own with greater propriety than those centering about the functional analysis of the peripheral nervous system. The recent phase of this movement may be said to date from the suggestion of OSBORN in 1888 of the possibility of an anatomical correlation of certain components of the peripheral nerves and their end organs with corresponding centers within the brain, a correlation of which we had at that time only vague hints. This suggestion was taken up and first worked out in a concrete case for the cranial nerves by STRONG in 1895, and since that date has dominated most of the really valuable morphological work on the peripheral nerves; in fact it is safe to say that no investigators in this field who have neglected to take account of this point of view have been

able fully to enter into their own data. Already some dozen researches have appeared in this country largely inspired by this point of view, which has, however, been generally ignored abroad save for the admirable studies of COLE of Liverpool.

We may, then, claim for the doctrine of nerve components as comparatively studied that it is distinctly an American contribution to neurological science. It is not necessary in this place to enter into an exposition of what that doctrine is, for this has been done *in extenso* in the address printed in our issue for last December. What we wish here to emphasize is that, apart from its great morphological value in determining homologies and critically defining the proper use of the cranial nerves in attacking such problems as the segmentation of the vertebrate head and its relation to the trunk, etc., perhaps its chief interest and value lie in the fact that it opens a very attractive avenue for the study of the physiological subdivision and interpretation of the entire nervous system, both central and peripheral.

In fact the whole point of this series of researches from the beginning has been the accurate demarcation of functional systems of neurones as the real units of the nervous system. Starting at the periphery where the functions of the terminal organs of the nerves are either well known or open to direct experimental determination, the conduction pathway is followed proximally into the brain and through its devious ramifications within that organ. Ultimately when each such functional system is exhaustively known we shall have the anatomy and physiology of the central, as well as the peripheral, nervous system well outlined and, when this knowledge is made comparative, the materials for a complete phylogeny of the nervous system.

The great problems of evolution, when finally solved, must be stated in functional terms. It is the problem of evolution to determine not merely what has been the history of the structural metamorphosis of organs and species, but what have been the dynamic factors which have shaped that metamorphosis, what influences of environment and internal organization have

been operative at each successive evolutionary stage to determine the next step to be taken.

In the doctrine of nerve components as it is now being wrought out we have a concrete illustration of the correlation of structural and functional data and methods in the solution of some of the greater problems of vertebrate descent, and especially in the interpretation of the human nervous system, the culmination of that evolutionary history. We shall be able to present from our contributors illustrations of the practical workings of this principle in detail within a few months.

RECENT STUDIES ON THE FINER STRUCTURE OF THE NERVE CELL.

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The finer structure of the nerve cell remains the object of study for numerous investigators. Interest centers here from many points of view. From the physiological view-point there is sought the correct differentiation of the protoplasm from the metaplasm and the determination of the relation which each of these, in its various aspects, holds to the activities of the cell. The pathologist demands, further, the structural basis and explanation of the various morbid activities as distinguished from each other and from the normal. And for the morphologist the subject presents a variety of problems which may be approached by both comparative and embryological methods.

In a field of so varied interests and in which at the same time there is much diversity of opinion, the results from various sources must undergo frequent critical analysis and synthesis. In no other way can the general trend of facts be discovered and progress in the subject as a whole be measured and made useful. With this thought in mind I have undertaken to study such recent papers and monographs relating to the structure of the nerve cell as were available and to bring together synthetically the opinion of different authors under topics which appear to hold important place in the minds of investigators.

The discussion is arranged according to the following plan:

- Ground Substance and Neurofibrillae
- The Moniliform Condition of the Dendrites
- Golgi's Endocellular Net
- The Gemmules
- Golgi's Pericellular Net
- Intracellular Canaliculi
- The Nucleus
- The Nucleolus
- The Centrosome
- The Tigroid Substance and Chromatolysis

The Ground Substance and Neurofibrillae.

The challenge which came to the neurone theory through the works of ΑΡΆΤΗΥ and BETHE has awakened new interest in the finer structure of the cytoplasm of the nerve cell. That there are structures in the properly fixed and stained neurone, especially of invertebrates, which accord with the neurofibrillae of these authors can no longer be doubted. But the exact relation which these fibrillae hold to the protoplasm of the living cell, to the inter-relation of neurones, and, therefore, to the conduction paths of the nervous system, is not satisfactorily explained. Is the neurofibril a protoplasmic thread or is it a derived substance of the protoplasm as PUGNAT and others argue? If it is a derived substance, it may well pass beyond the limits of the cell and form extra-cellular nets in the neuropil, as BETHE and ΑΡΆΤΗΥ and their followers describe. But if the fibril is protoplasmic its nature excludes the possibility of such nets since the limits of the cell would coincide with the limits of the protoplasm. But if the fibril be protoplasmic, are there structural features of the cytoplasm by which the origin, development and final behavior of the fibril can be explained? Towards the answer of such leading questions, some of the following works contribute in a positive manner.

HOLMGREN ('99), in his monograph upon the spinal ganglion cells of *Lophius*, does not commit himself to a definite statement regarding the ultimate structure of the cytoplasm. He describes however, a certain radial appearance about the nucleolus in its migration from the nucleus into the cytoplasm which he considers suggestive of the alveolar structure. Yet his figures and descriptions in general do not seem to sustain this interpretation throughout. In his beautifully executed drawings (Taf. IX-X, Fig. 3) he represents the cone of origin as marked with stripes which are directed from the axone into the cell body. In the more distal part of the cone these stripes seem to form elongated and very narrow meshes. As the structure recedes into the cell body the meshes become shorter and broader, and especially is this true in the peripheral region of the cell where the meshes become very irregular in shape and size. Though HOLMGREN does not discuss this structure in detail as related to the structure of the cytoplasm his figures are strongly suggestive of the cytoplasmic reticulum as described by HATAI and others.

In a later work upon the structure of the nerve cell HOLMGREN ('00) finds more positive data on this feature of the neurone. He demonstrates a fibrillar structure which he considers identical with the fibrillar substance of FLEMMING. The fibrillae of the cytoplasm are

continuous with those of the axone, but none of them anastomose. They follow an undulating or somewhat spiral course through the cell body, with a tendency to be more nearly parallel in the peripheral zone. The interfibrillar substance is homogeneous.

But the fibrils of this net, it is important to notice, are to HOLMGREN the neurofibrillae. In both vertebrates and invertebrates they may enter or leave the neurone at any point in the periphery of the perikaryon or of the processes. Furthermore, Holmgren says, "die wabige, pseudowabige oder spongioplasmatische Structur, wie man sie auch nennen will, die ich bei *Lophius*, die RAMÓN-Y-CAJAL, LENHOSSEK, VAN GEHUCHTEN u. A. beschrieben haben, nur einem accidentellen Aussehen der resp. Zellen entspricht, im besten Falle durch einen gewissen physiologischen Zustand hervorgerufen." That is to say, the "filare Substanz" of FLEMMING is resolved by HOLMGREN into the neurofibrillae of APÁTHY and BETHE, and the structural parts of the ground substance, such as granules, trabeculae etc., of many authors are interpreted as functional or artificial modifications of FLEMMING's amorphous "interfilare Substanz."

KOLSTER's monograph upon the nerve cell of *Petromyzon* contains an interesting demonstration of certain features of the ground substance. KOLSTER has made an exhaustive study of unstained preparations of the nerve cell mounted in media of various refractive indices, and also of unstained osmic acid preparations. In none of his mounts made by these methods has he found anything akin to a fibrillar or reticular structure. But in cells preserved in FLEMMING's solution for several months or even for more than a year, and subsequently stained in saffranin and differentiated in a 20% tannin solution followed by absolute alcohol, he discovers very fine lines running through all the cytoplasm. These lines are made up of a single row of dark red granules which the author treats as microsomes. In some of his figures these lines seem to form a net with relatively large, irregularly shaped meshes, but the author believes that anastomoses between the lines are relatively rare. In thick sections these granules appear large, but thinner sections show that these relatively large granules are made up of short rows of exceedingly small granules running in all directions. The whole structure, then, is resolved into a network of microsomes in linear arrangement. Furthermore, KOLSTER demonstrates that this net is concentrated into a dense granular mass directly around the centrosphere, where a granular effect is given in unstained preparations. From this central mass rather thick rays extend in different directions, and these fray out into the fine lines of

microsomes. KOLSTER interprets this structure as different from anything that had been previously described, but it would seem to be indistinguishable from the neurosomic net met with by other authors.

According to BOCHENEK ('01) a fibrillar net may be beautifully demonstrated in the nerve cells of *Helix* by the gold chloride method. In the body of the cell the meshes of the net are triangular or polygonal but in the axone hillock they elongate. The fibrillae which course independently through the axone are continuous with the fibrillae of the net. The author finds it impossible, however, to distinguish between the motor and sensory fibrils. He finds, also, that the net in *Helix* is much more dense than it is in the nerve cells of *Lumbricus*. He interprets this as indicating a higher state of organization in *Helix*, which would be, in respect to the degree of differentiation of the intracellular net, intermediate between *Lumbricus* and the vertebrates. BOCHENEK treats this net as "un réseau protoplasmatique."

VAN GEHUCHTEN, in his earlier work ('97) upon the internal organization of the nerve cell, took the position that the ground substance of the cytoplasm consists of a fibrillar net suspended in an amorphous fundamental substance. This net extends into the process in the form of elongated meshes which superficially give the appearance of distinct fibrils. These two elements are considered by VAN GEHUCHTEN "le véritable protoplasme de la cellule nerveuse." The net or organized part he homologizes with the "masse filaire" of FLEMMING. In a later work ('98), published jointly with NELIS, VAN GEHUCHTEN quotes FLEMMING as coinciding perfectly with this interpretation as given in 1897. The authors, however, proceed at once to modify their interpretation in certain details. They found certain spinal ganglion cells of the rabbit which, because of the absence of chromatic substance in the peripheral region, gave excellent advantages for studying the achromatic structure. In these cells, by the use of toluidin blue and erythrosin, they found the net to be made up of granules united together by thin trabeculae of the same substance. But they add: "Le réseau protoplasmatique qui existe indubitablement dans toutes nos préparations diffère totalement des fibrilles courtes, flexueuses, irrégulières et indépendantes décrites et figurées par FLEMMING." He believes also that the net differs clearly from the net described by DOGIEL and that it is much more regular than that figured by MARINESCO.

In regard to the cone of origin, also, the authors have changed their views slightly. Instead of the comparatively thick and regular

fibrillae which most authors describe, VAN GEHUCHTEN and NELIS find a delicate, granular striation which they fail to connect certainly with the cytoplasmic net. The granules of the striae are so arranged as to give in some cases a cross-striated effect.

PATON ('00), in his studies of the neurofibrils of the cerebral cortex of the pig, finds that the fibrillae of the axone run independently of each other into the cell body, where they enter into a most intricate net-work. He holds that the fibrillae of this net are continuous with those of a pericellular reticulum, which he interprets as identical with GOLGI's pericellular net.

PATON believes that the fibrils are very quickly affected by post-mortem granular disintegration which begins at the center of the cell. He believes this fact may account for the view of certain authors that fibrils exist only in the apical process of the cell.

PRENTISS has recently published in this Journal his latest results upon the neurofibrillar structures in *Hirudo* and *Asticus*. As to the general arrangement of the fibrils in the cell body he confirms APÁTHY's position. He concludes, however, that "Neither in vertebrates nor in crustacea do the neurofibrillae of the nerve cells show any marked correlation in size and function." He believes that the differences in size which APÁTHY observed are due to incomplete impregnation of the fibrillae and perhaps to the cleaving together of smaller fibrillae in the cell process. As to the relation of the fibril to the cell and its processes PRENTISS supports BETHE's view that fibrils may enter one process and leave by another or by a collateral without coming into relation with the perikaryon itself. In *Hirudo* he finds a very limited fibrillar network in the neuropil. Such nets are more extensive in *Astacus* but they are not diffuse in their relation. They put relatively few fibrillae into communication with each other. PRENTISS considers that his preparations tend to confirm BETHE's theory that the cells are not the centers of nervous activity, and that the fibrillae are continuous from cell to cell.

PUGNAT, in his recent review on the finer structure of the nerve cells, comes to the conclusion that the formed substance of the cytoplasm is a net, in some cases of fibrillae, in others of trabeculae, and that this net is continuous with the fibrillae of the processes of the cell. The relation which this net holds to the life and function of the cell, he thinks, can best be explained upon BARD's theory of "derived substance." Although PUGNAT does not accept the sharp chemical and physical distinction between the protoplasm and the derived substance as BARD proposed, he believes that fibrillae are a product of the

protoplasm, that they are the conducting element and are therefore the seat of katabolic processes, while the protoplasm and nucleus are the seat of the anabolic process. How the fibrillae are repaired by the protoplasm, PUGNAT says, we are absolutely ignorant. Through this theory of derived substance PUGNAT attempts to bring the neurone theory into harmony with the results of APÁTHY and BETHE and their followers. He thinks that whether the fibrillae as derived products of the cell are continuous or not from cell to cell, the nerve cell itself may be considered as an anatomically distinct unit. He would, in other words, place the neurofibrillae in the same category with the fibrillae of the muscle or connective tissue cell. However, before such a compromise of the neurone theory is conceded HATAI's methods, by which he has received such brilliant pictures of the finer structures of the nerve cells and of the axone terminals, must be given a thorough test. The results which he has recently published are remarkably convincing.

In the afferent neurones of the electric lobe of *Torpedo* HATAI ('01) demonstrates fine fibrillae in enormous numbers, crowding the cell processes and the perikaryon. By serial sections through one of these large cells he shows the behavior of the fibrillae within the cell body. Upon emerging from the process into the cell body they diverge in clusters. Some sweep around the nucleus to form here a dense net, others pass to various processes of the cell in such a manner that there is direct fibrillar connection established between each dendrite and every other dendrite and between the axone and all the dendrites. By this coursing of the fibrillae from the dendrites into the axone there is a beautiful spiral configuration given to the ground substance of the cone of origin. Superficially HATAI's figures in this case have a striking resemblance to the familiar drawing of the fibrillar elements in the nerve cell by MAX SHULTZE.

HATAI, however, makes an important step in advance by demonstrating that these same fibrillae in the electric neurones of *Torpedo* can be resolved into rows of neurosomes. Furthermore, he asserts that these neurosomic fibrils in reality are a modified reticulum. It is only in thicker sections and under lower magnification that the structure gives the fibrillar appearance.

HATAI has demonstrated the reticular structure more exhaustively in the nerve cells of the white rat. He has studied these cells ('03) by the methods of BETHE and DOGIEL, but finds no such fibrillar structures as they describe. On the other hand, he demonstrates by other methods a neurosomic reticulum which is modified into a pseudo-

fibrillar structure. The fibrillae are made up of rows of neurosomes connected by slender protoplasmic filaments. Generally, around the periphery of the cell body the meshes are larger than in other regions. Around the nucleus and in the cone of origin they become more narrow and very much elongated. A more pronounced modification of this character is found in the axone so that the reticular condition is difficult to see. In the axone, however, the neurosomes stain brighter than elsewhere. Especially is this true of the neurosomes of the axone terminals, where they are also larger than in other parts of the cell. The dendrites contain a relatively small amount of the ground substance and the neurosomes stain more faintly than in the axone. This fact enables HATAI to differentiate the finest dendritic branches from the contiguous terminals of the axone. Even in the gemmules he demonstrates the neurosomic reticulum as continuous with that of the rest of the cell, but he finds that its neurosomes differ both in size and staining reaction from those of the axone terminals. He concludes that there is no continuity of the so-called fibrillar structures between the nerve cells.

Now HATAI finds that a number of these neurosomic filaments may mat together into thicker strands and that several of these strands in some cases form a complicated network around the nucleus. Such a network does not appear in the cone of origin or in the periphery of the cell body. He homologizes this network with the intracellular anastomosing fibrils of APÁTHY and also with the endocellular network of GOLGI. Thus HATAI resolves the neurofibrils of APÁTHY into the protoplasmic elements of the cell and denies that they pass continuously from cell to cell. The diffuse nets in the neuropil and pericellular nets also may be resolved into the reticulum of axone terminals which would be strictly protoplasmic and not extra-cellular, derived substance.

Moniliform Condition of the Dendrites.

Since DOGIEL's discovery of the dendritic varicosities in the cells of the retina this feature of the nerve cell has held an important place in neuro-cytology. Among the most comprehensive contributions upon the subject are those of SOUKHANOFF. This author made four experiments by ligature of the abdominal aorta, three upon guinea pigs which died from the experiment in from one-half to twenty-four hours, and one upon a rabbit which was killed after twenty-four hours. In these experiments he found that the diminished blood supply had produced a very rapid modification in the nerve cell, varying directly in

intensity with the duration of the anemia. The modifications of least intensity consisted in the appearance of swellings along the dendrite which made its contour irregular. As this condition became more intensified the swollen regions of the dendrites became fusiform and then spherical. During this process the connecting regions between the enlargements of the dendrites became more attenuated till a final beaded or moniliform condition resulted. This modification he considered pathological.

In another article ('98) upon the modification of the dendrites under the influence of narcotics SOUKHANOFF reports in considerable detail the results of nine experiments upon mice, rabbits and guinea pigs. These animals had been subjected to the vapor of ether, chloroform or alcohol for various periods of time. Two of the experiments were made by injection of trional. As a result of these experiments and of a critical review of the work of other investigators, SOUKHANOFF draws the following conclusions: (1) The moniliform condition may occur in certain dendrites under normal conditions, a conclusion reached by practically all authors; (2) under the influence of ether, chloroform or alcohol there is not a very appreciable increase in the moniliform condition; (3) injection of trional causes a moniliform condition of nearly all the dendrites of the cerebral cortex; (4) this change is accompanied by a more or less complete loss of the gemmules; (5) a loss in weight in guinea pigs subjected to trional injections can be attributed only to profound nutritive derangement. This suggests that the moniliform condition of dendrites may be "une degenerescence sui generis" manifested whenever nutrition is severely affected.

A third contribution by SOUKHANOFF ('98) deals with the varicose atrophy of the dendrites in the cerebral cortex under pathological conditions. His pathological studies were checked by examination of a normal specimen. From an exhaustive study of the latter case he concluded that the moniliform condition of the dendrites is occasionally found under normal conditions, but that it is very slight and not to be compared with that found in cases of poisoning. From nine experiments upon guinea pigs which had been subjected to arsenic poison in varying degrees for periods of from six to thirty-three days, he concludes that in acute and subacute poisoning by arsenic there occurs a moniliform degeneration of the dendrites of the cerebral cortex. This is very slight in some cases, but very marked in others. This difference cannot be accounted for by difference in the duration of the poisoning. Its cause is more likely to be found in individual differences in the specimens as regards resistive power and general health.

SOUKHANOFF's experiments include also poisoning by rabies and tuberculin and a case of thyroidectomy. In a rabbit infected with rabies during eighteen days and fatally, the varicose degeneration of the dendrites was slight. The experiment upon the influence of tuberculin was performed upon a dog that had some time previously been inoculated with tuberculin for immunization. It was then inoculated with an emulsion of the *Bacillus of KOCH*. From his study of this case SOUKHANOFF concludes that the varicose condition occurs in many dendrites of the cerebral cortex but that this is due to derangement in nutrition. In the case of thyroidectomy, upon a dog which lived a week after extirpation of the thyroid gland, profound changes were observed in both large and small dendrites of the cerebral cortex. This also SOUKHANOFF attributes to nutritive derangements which are known to follow thyroidectomy.

In general SOUKHANOFF concludes that although some dendrites in the normal nervous system are found in the varicose condition, the large numbers found changed under certain conditions are indicative of a morbid process; and that all poisonings which cause profound derangement in general nutrition cause a pronounced varicose degeneration of the dendrites.

The condition of the dendrites in the spinal cord of the rabbit has been studied by SOUKHANOFF and CZARNIECKI ('02). The spinal cord of two specimens, which were killed quickly with chloroform were treated by the GOLGI method. To bring about quicker penetration of the fluid incisions were made along the cord. The authors find that the cells of the cord show very pronounced differences in the form of the dendrites. The cells of the anterior horns differ strikingly in this respect from all other cells in the cord. Some of the dendrites of the anterior horn cells have comparatively regular contour, others are in a distinct varicose condition while the majority are in a condition intermediate between the two extremes. On the other hand, the dendrites of many of the small cells of the cord were found in a very marked varicose condition.

GEIER ('01) reports a series of experiments which are especially noteworthy for their thoroughness. They were made upon mammals and birds killed with chloroform or ether, and involved an examination of at least an entire cerebral hemisphere in each case. He describes each case in detail and draws the general conclusion that anesthesia by chloroform or ether does not of itself cause a moniliform condition of the dendrites, but that such a condition must be considered as the expression of a morbid or fatigued state of the cell. He holds also that the

moniliform condition is not an expression of the plasticity of the cell as certain authors have claimed.

In a later contribution GEIER ('02) presents important data upon the development of the protoplasmic processes as well as upon their form in the adult. He has studied by the GOLGI method the cells of the spinal cord of rabbits of different ages; one day, two weeks and one month; and of kittens at birth and at three days, seven days, one month and two months old. The two series of experiments lead to the same conclusions: the protoplasmic processes of the anterior horn cells are less regular in outline in the new-born than in the adult. As the animal grows the outline of the processes become more regular and the process straightens. In the new-born the dendrites have a more regular contour in the region of the cell body than in the distal region, and the process of straightening progresses from the cell body outward. As for the dendrites of the posterior horn, GEIER finds it difficult to determine whether there is any such change accompanying growth as he describes for the anterior horn cell. This difficulty arises from the fact which he demonstrated in his earlier work and which his present investigation confirms, that the dendrites of the posterior horn of the adult are normally very irregular in outline as compared with the dendrites of the anterior horn cells. He finds, however, that there are certain cells in the anterior horn which have very irregular dendrites. He considers them commissural cells. In his youngest specimens he found the varicose condition of the dendrites very conspicuous, but less marked in the older specimens. The condition tends to disappear as the animal grows.

Golgi's Endocellular Net.

SOUKHANOFF ('02) has made a specific study of GOLGI's endocellular net in the cells of the cerebral cortex of mammals by modifications of the GOLGI method. He finds this net only in a zone around the nucleus, although it does not lie directly upon the nucleus. Surrounding the net is a zone of protoplasm which is noticeably clearer than the rest. Some of the filaments of the net are fine, others are coarse, still others are ribbon-like. Often they are of irregular contour. In some small cells the net consists of only a few curls of the filaments, and it is a much simpler structure in the cortical cells than it is in the cells of the cord and spinal ganglia. In general form the net conforms rather closely to the shape of the cell. Sometimes one branch of the net, sometimes two or three, pass out into the process.

In the interpretation of the endocellular net SOUKHANOFF speaks

positively on three points: it is a strictly endocellular structure; it has nothing to do with the neurofibrils of APÁTHY and BETHE; it is not identical with the canaliculus HOLMGREN. Regarding its relation to "l'état spiremateau" of NELIS, he could not at the time of writing offer a positive opinion.

As already stated in the discussion of the structure of the ground substance, HATAI ('03) resolves the net in question into a modified protoplasmic reticulum. His position upon this point is strongly supported by almost every feature of the net which SOUKHANOFF emphasizes,—the lack of uniformity in size and the irregularity in contour of the fibrils, the restricted perinuclear position of the net, its conformity in shape to the shape of the cell and its relation to the processes of the cell. In all of these features the net has a striking resemblance to the filaments which HATAI describes as formed by the matting together of numerous fibrillae of the neurosomic net. But it will be remembered that HATAI considers that the neurofibrils of APÁTHY are identical with this modified reticulum. The interpretation would place him in direct opposition to SOUKHANOFF when the latter says that the GOLGI endocellular net has nothing to do with the neurofibrils of APÁTHY and BETHE.

By HATAI'S work, therefore, another of the manifold structural elements of the nerve cell is explained upon the basis of the fundamental structure of the protoplasm.

The Gemmules.

The structures which BERKELEY called "gemmules" have received various names by other investigators: "épinés" by RAMÓN-Y-CAJAL; "appendices piriformes" by MŁLE. STEFANOWSKA; and "appendices collatéraux" by others. As treated by many authors they may vary in form from short club-shaped to spindle-shaped or even filamentous structures. In his study of the cellular changes in the cerebral cortex under experimental anemia, SOUKHANOFF ('98) finds that as the symptoms become more acute the gemmules become modified and ultimately disappear. In another work of the same year, he discovered similar changes in the gemmules in animals which have been subjected to the vapors of ether, chloroform and alcohol. In other animals treated with injections of trional the pronounced modifications in the gemmules, as well as other changes in the central system, were attributed to the derangement of general nutrition and not to the specific action of the drug.

In further pathological studies with the GOLGI method, SOUKHAN

OFF ('98) observes that the gemmules are lost in varying degrees in the nerve cells of animals subjected to poisoning by arsenic, rabies, tuberculin and also of animals suffering from thyroidectomy. These studies were checked by preparations of nerve cells from a normal guinea pig killed by decapitation. The nervous tissue was quickly placed in the fixing reagents and received like treatments with the abnormal tissues. The preparations showed gemmules present almost universally upon the dendrites.

In collaboration with CZARNIECKI, SOUKHANOFF ('02) has studied the dendrites of the ventral horn cells of the rabbit with the GOLGI method. By killing the animals quickly with chloroform the authors considered that the tissue was found in the normal condition.

Upon the dendrites of certain cells very few gemmules were found; in others they were numerous, beginning to appear on the dendrites nearer the cell body and becoming more numerous as the distance from the perikaryon increased till in the distal region they almost covered the process. In another type of cell, which lay with the protoplasmic processes partly within the white substance, that part of the dendrite which lay within the white substance bore no gemmules, while the part lying within the grey substance was abundantly supplied with them. And even when the dendrite lay in the border line between the grey and the white substance the side of the dendrite which faced the grey bore more gemmules than did the side facing the white. The authors conclude that the gemmules are much less numerous upon the ventral horn cells than upon the cells of the cerebral cortex, but that they are much more variable in size and shape. They may be pyriiform, filamentous, club-shaped, tubercular, or finely branched. Certain of these forms which the authors call "rejitons," which are very irregularly fibrillar and club-shaped, are not found in the cells of the cerebral cortex.

GEIER ('01) has studied with the GOLGI method the cerebral cortex of mammals and birds which have been subjected to the vapors of ether and chloroform for from five to ten minutes. In some of the experiments the gemmules showed a tendency to disappear, while in others the cells appeared perfectly normal. The disappearance of the gemmules was found to be concomitant with the moniliform condition of the dendrites. As GEIER considers the moniliform condition of the dendrites as morbid, due probably to exhaustion or want of nutrition, he would also interpret the disappearance of the gemmules as indicative of morbid processes in the cell.

In a later work GEIER ('02) described the development of the pro-

toplasmic processes of the cells of the spinal cord of the rabbit and cat. Besides the ordinary club-shaped gemmules there are others, in the animal just born, in the form of fine filaments or spines which often arise from a small conical projection of the dendrite. In the middle of this filament may sometimes occur a small thickening. The processes of the posterior horn cells have the same type of gemmules but have them in much larger numbers.

In a rabbit two weeks old the processes have become more regular in outline. This change appears only in the basal part of the dendrites and advances with age towards the periphery. The filamentous gemmules do not appear at this stage all along the dendrites as they did in the rabbit one day old, but occur only in the more distal, irregular part of the process. In a rabbit one month old they are found only on the extreme terminal branches of the dendrite. In cats from birth to one month old the same mode of development is followed. But in kittens two months old GEIER found no typical filamentous gemmules upon the anterior horn cells. In place of them were similar processes of much larger size. This, together with the fact that in an animal three days old the filamentous gemmules are two or three times larger than they are at birth, indicates that some at least of these gemmules grow into dendritic branches. GEIER believes that all such gemmules of the young cells are dendrites in the process of development.

This peculiar type of gemmule is not found upon the posterior horn cells, but the more complex forms are very abundant on the dendrites and occur also on the cell body. GEIER concludes that the gemmules are relatively rare upon the anterior horn cells and of a constant form while they are exceedingly numerous and variable in form upon the cells of the posterior horn. Their absence in any case is associated with the moniliform condition of the dendrites.

PATON ('00) interprets the gemmules as artifacts which mark the points at which the fibrillae of the pericellular net enter the cell or come in contact with it. He asserts that the appearance of the gemmules upon the cortical cells of the embryo is synchronous with the appearance of neurofibrils.

That the gemmules mark the point of continuity between the intracellular and the pericellular fibrils is denied by HATAI. He demonstrates the neurosomic net within the gemmule and the neurosomic nature of the axone terminals which compose this pericellular net. But, while the two fibril systems come into intimate touch with each other, especially at the gemmules, they differ sufficiently in structure

and reaction to enable one to determine a boundary line between them.

As to the physiological significance of the gemmules, their finer structure and their reaction to anesthesia as well as the features of their distribution as noted above, would seem to justify us in according to them an important part in the maintenance of the conduction paths within the central system.

Golgi's Pericellular Net.

The network of fine fibers which GOLGI first described as surrounding the nerve cells of the central and peripheral system has been treated by subsequent writers as both nervous and non-nervous. The more recent work, however, by HELD, BETHE and others demonstrates that this net is continuous with the terminals of medullated axones. HATAI ('03) confirms this position and shows further that the fibrillae of the net are of the same nature as those of the axone. That is to say, they are a modified neurosomic reticulum. We have treated the relation of the net to the nerve cell in the foregoing section upon the gemmules.

HATAI's observations would seem to be in harmony with HOLMGREN's ('99) views regarding the pericellular net of the spinal ganglion cell of *Lophius*. This net lies between the capsule and the cell and between the lamellae of the capsule. It is continuous with fibers which come from other regions of the spinal ganglion and with fibrils which penetrate deeply into the cell. But these fibrils do not become continuous with the protoplasm of the cell into which they penetrate. A light area always separates them from the surrounding protoplasm.

Intracellular Canaliculi.

In 1886 FRITSCH first discovered an intracellular system of vessels in the nerve cell. His observations were made upon certain large cells in the medulla of *Lophius*. He interpreted the structures as genuinely vascular. HOLMGREN ('99) discovers similar structures in the spinal ganglion cell of *Lophius* and claims that he is first to confirm the observations of FRITSCH. But during the same year of HOLMGREN's publication NELIS ('99) introduces "un nouveau detail" in the protoplasmic structure of the nerve cell, which has many features in common with the intracellular vessels of FRITSCH and HOLMGREN. These structures, the "Gefässe" of FRITSCH, the "Kanälchen" of HOLMGREN and "l'état spirematureux" of NELIS, we shall for convenience designate as intracellular canaliculi.

HOLMGREN ('99, '00) asserts that the canaliculus is continuous with the pericellular lymph space and that it is accompanied by trabeculae of the connective tissue capsule of the cell. Along with it occur also the nuclei of its membranous walls and connective tissue nuclei which have migrated in from the capsule of the cell, while corpuscles of the lymph circulate through the canaliculus.

KOLSTER ('00) observes canaliculi also in the nerve cell of the spinal cord and spinal ganglia of *Petromyzon*. He has demonstrated them successfully in unstained sections of cells fixed in osmic acid. He traces them from the periphery of the cell into the deepest part where they seem to be continuous with a perinuclear space of the same nature. A slight invagination of the endothelial capsule may occur where the canaliculus enters the cell and free nuclei are found in the protoplasm which are interpreted as nuclei of the capsule; but KOLSTER, even with the technique employed by HOLMGREN, fails to find a nucleated membranous wall surrounding the lumen of the canaliculus. It is bordered simply by the granular protoplasm of the cell. Still, in a later work, HOLMGREN ('00) confirms his first observations by demonstrations of the canaliculus in the nerve cells of mammals and birds with all the features originally described for *Lophius*. He further shows that electrical stimulation of the nerve cell causes an expansion of the canaliculi.

HOLMGREN's interpretation of the canaliculi receives positive support from the observations of PUGNAT ('01) upon the embryological development of the canaliculus in the nerve cell of the chick. PUGNAT finds that the canaliculi appear first in the outer zone of the spinal ganglion cell on the eleventh day. By the fifteenth day they have reached the central zone. These canaliculi, according to PUGNAT also, have membranous walls and are continuous with extracellular vessels of the same nature.

Canaliculi have been recognized also by BOCHENEK in the largest nerve cells of *Helix*. As to the structural and topographical features of the system, BOCHENEK agrees in the main with HOLMGREN. He finds the connective tissue fibrillae and cells very conspicuous in the protoplasm of the nerve cell and even invading the basal portion of the axone. He explains the structure as a simple invagination of the capsule into the body of the nerve cell or as clefts in the cell. His figures and descriptions would not give one the idea of a clearly defined membranous wall about these clefts, yet he says "Si, dans cet exposé des faits, nous sommes en complet accord avec le travail de HOLM-

GREN, nous ne pouvons pourtant pas souscrire a ses déductions théorétiques."

The theoretical deduction of HOLMGREN to which BOCHENEK cannot subscribe is regarding the significance of the canaliculus in *Helix*. HOLMGREN holds that the nerve cells are poorly or richly supplied with canaliculi according to the functional condition. BOCHENEK has observed, however, that the canaliculi of *Helix* are equally developed in winter and in summer; that is, during the periods of activity and inactivity. He believes, therefore, that they are constant features and are to be explained as an adaptation of a large cell for increased absorbing surface.

The "nouveau détail" which NELIS ('99) calls "l'état spiremateux" is in the form of a spireme-shaped or much coiled, continuous band. In material hardened in GILSON'S fluid or 5% formalin and stained in HEIDENHAIN'S iron haematoxylin and eosin or erythrosin these bands appear uncolored and amorphous, and marked off from the colored ground substance by regular, parallel lines. The position of the spireme varies in position and extent in different cells. It may lie near the periphery of the cell, near the center or in close relation to the nucleus. In some cases one of its borders is indistinguishable from the nuclear membrane; although the author considers that the two elements do not in reality coincide.

NELIS finds the spireme in the plexiform ganglion of the dog, and, less conspicuously, in the superior cervical ganglion. It is present in the pyramidal cells of the cerebral cortex and in the spinal ganglion cells also. He considers that this is a normal structure, but that under certain pathological conditions it may become much more extensively developed and more easily demonstrated. As to its significance, NELIS is undecided, but he is inclined to interpret it as a protoplasmic element of the cell.

DE BUCK and DE MOOR ('99), in a work upon the lesion of the nerve cells accompanying experimental tetanus in the guinea pig, find a system of vacuoles which they identify with the spireme of NELIS. These vacuoles may approach very near the border of the cell, but are always separated from it by a thin layer of protoplasm. VAN GEHUCHTEN and NELIS ('00) have observed the structure also under pathological conditions and conclude that it is accentuated by arsenic poisoning, tetanus, etc.

Among these various descriptions of intracellular vessels it is quite easy to identify the type described by KOLSTER with the canaliculus of HOLMGREN, by assuming that KOLSTER has failed to demonstrate the

membranous walls of the vessel. Furthermore, the general form and position of the spireme of NELIS harmonizes well with the canaliculus of HOLMGREN. Though NELIS does not find nucleated membranous walls, he does find parallel walls with a sharp contour. It only remains to demonstrate the continuity of the structure with extracellular lymph vessels in order to identify it with the canaliculus of HOLMGREN. But as to the interpretation of BOCHENEK's clefts we find greater difficulty. He has compared his preparations with the original preparations of the spireme made by NELIS and has decided that the two structures are totally different. He expresses himself as surprised, also, that HOLMGREN should homologize the canaliculi of *Helix* with the spireme. This suggests that HOLMGREN and BOCHENEK may be dealing with altogether different structures. It may be that BOCHENEK has not seen the genuine canaliculus with membranous walls, but that he has demonstrated only deep clefts in the cell which are filled with the capsular tissue.

The Nucleus.

HOLMGREN ('99) finds that the size of the nucleus in the spinal ganglia of *Lophius* varies with the size of the cell. The linin net and chromatic granules, which stain red with toluidin blue and erythrosin, are massed thickly around the nucleolus and radial branches stream out from this to the nuclear membrane which is acidophile also. On the side of the nucleus which lies nearest the center of the cell the contour may become flattened or even indented by a mass of tigroid substance which accumulates at this point. The nuclear membrane of this region thickens and changes its reaction to the stain, for it now stains dark blue in toluidin-erythrosin, deep black in iron haematoxylin and green with the triple BIONDI stain. Simultaneously with this change in the nuclear membrane there come changes in the tigroid mass, which is heaped upon the nucleus in this region. The large tigroid bodies, which, earlier in the process, were packed closely together here, have become resolved into small granular heaps or scattered granules suspended in a homogeneous or purely granular ground substance. The latter stains blue with toluidin-erythrosin, gray or perhaps black with iron haematoxylin and red with the triple acid stain. Following this condition the thickened part of the nuclear membrane disappears either throughout the entire extent or at intervals. Through this cleft the cytoplasm becomes continuous with the karyoplasm. The union takes place through protoplasmic bands (Züge) which radiate from the centrosome into the nuclear substance and become continuous

with the linin net. The part of the linin net which enters into the radiating bands contains granules which stain a darker red than the other acidophile elements and black with iron haematoxylin. In the radiating bands beyond the limits of the nucleus there occur granules which stain black also in iron haematoxylin but dark blue in toluidin-erythrosin. They are sharply differentiated from the tigroid elements by their reaction to DELAFIELD's haematoxylin and the triacid stain. In the former they stain blue-black, while the tigroid elements stain faint blue; in the latter, they appear green while the tigroid elements appear red. This reaction places them in the category of basichromatin and they must be considered as such elements which have migrated out from the nucleus. They become basophile during their migration from the nucleus and represent the nuclear chromatin.

While these changes are going on the nucleus enlarges and migrates towards the periphery of the cell, till, in some cases, a mere film of protoplasm separates it from the cell membrane. In the meantime, also, the acidophile granules of the nucleus have increased greatly in number and during the process also the nucleolus sends off fragments into the cytoplasm.

KOLSTER ('00) also contributes interesting facts upon the general morphology of the nucleus. In a large series of preparations he finds that only a part of the nuclear border has a regular outline and limiting membrane. As studied in serial sections the nuclei, practically without exception, lose their membrane in a particular region and the karyoplasm pushes out in pseudopodia-like processes into the cytoplasm. This appears to the author to be a constant feature and not due to any peculiar physiological condition. He interprets it as concerned in the nutrition of the nucleus. But, compared with HOLMGREN's work, KOLSTER's results are noteworthy from the fact that the side of the nucleus which is marked by this irregular contour may lie opposite the centrosome while HOLMGREN finds it directed toward the centrosome.

Irregularities in the border of the nucleus have been observed also by BOCHENEK ('01) in certain large nerve cells of *Helix*.

The idea that the nuclear membrane breaks down and that there is an interchange of formed substance between the nucleus and the cytoplasm, especially as described by HOLMGREN, is opposed by SCOTT ('99). He believes this appearance is due to the action of the knife in cutting. However, it hardly seems probable that both HOLMGREN and KOLSTER should be utterly deceived in this manner. Moreover, it does not seem that SCOTT's fundamental thesis or his results

exclude the possibility of such ruptures in the nuclear membrane as HOLMGREN and KOLSTER describe.

The Nucleolus.

The behavior of the nucleolus in the spinal ganglion cells of *Lophius* as described by HOLMGREN ('99) has already been mentioned in the section relating to the nucleus. Regarding the finer structure and chemical nature of the nucleolus the works of KOLSTER, HATAI and SCOTT are noteworthy.

In the spinal ganglion cell and the FREUD' schen cells of *Petromyzon*, according to KOLSTER, the nucleolus appears homogeneous only in preparations fixed in sublimate and stained in iron haematoxylin. In all other methods which the author used he found two rather sharply differentiated zones, a dark, relatively large central portion surrounded by a shell of substance which stains more faintly than the central body. In some preparations there appeared a granular, intermediate zone between the central core and outer shell. KOLSTER is inclined to interpret the nucleolus, not as a solid mass, but as a vacuole with peculiar liquid contents. The reaction of the contents to reagents accounts for the structural features which appear by different methods. PUGNAT, on the other hand, considers that the central, granular appearance of the nucleolus is due to the presence of formed bodies.

SCOTT ('99) and HATAI ('03) both demonstrate an oxyphile center with basophile peripheral zone in the nucleolus. Only the basophile part represents the chromatin, while the oxyphile center is the true nucleolar substance.

The behaviour of the nucleolus of the nerve cell during mitosis has been carefully worked out by HATAI. While in the adult nerve cell the larger part of the nucleolus stains blue with toluidin-erythrosin, in the germinal cells the entire nucleolus stains a deep red. In the later telophase stage of mitosis the nuclear substance, which has become closely massed around the chromosomes, dissolves and accumulates again in small spherical masses which collect near the center of the nucleus. Each granule of this group sends out a process from either pole. These processes from the various granules anastomose to form a net with granules at the angles of the meshes. The linin and the basophile nuclear substance now collect around this group of acidophile granules to form the nucleolus of the adult nerve cell. But if the cell is to divide again, the linin which has accumulated around the nucleolus breaks up in the early prophase and the nucleolar granules separate. As the spireme forms they collect upon

it and ensheathes it, and form groups in the nuclear net. That which clings to the chromosomes become modified to form the "Halbspindel fasern." As the spireme splits, nucleolar substance still persists around the daughter spiremes. This tends to collect at the middle of the curved chromosomes which are turned with the convexity towards the centrosphere. As the daughter spiremes separate, nucleolar substance unites with the linin to form the rays of the central spindle. The linin in this phase stains slightly deeper than the cytoplasmic reticulum but not so deeply as does the nucleolar substance. It is only in the telophase stage that the nucleolar substance, which has been associated with the linin, becomes indistinguishable from it.

There seems to be conclusive evidence, therefore, that the nucleolus of the adult nerve cell is a heterogeneous structure with an oxyphile center which is structurally and chemically allied to the linin, and with a peripheral zone of basophile chromatin.

The Centrosome.

HOLMGREN finds that the centrosome in the spinal ganglion cell of *Lophius* is located in the center of the cell. It forms the center of the concentric circles and radial "Züge" of the cytoplasm. HOLMGREN suggests that, since its reproductive function must have ceased, and since it holds this constant relation to the trigroid substance, it is probably concerned in the nutritive functions of the metabolism of the cell. The object which LENHOSSÉK first interpreted as the centrosome in the spinal ganglion cell of *Rana* is, according to HOLMGREN, nothing other than a section through an invaginated trabecula of the capsule.

KOLSTER identifies the centrosome in the nerve cells of *Petromyzon* even in unstained preparations, but it is not located in the center of the cell. The centrosphere is surrounded by an irregularly shaped mass of granules which are arranged in the form of a dense reticulum, which we have already discussed in connection with the ground substance of the cytoplasm. The interior of the body in unstained preparations appears as dark, circular lines separated by bright points. In other methods, it appears as a circular space in which the centrosome lies.

The centrosome in the nerve cell of the dog and rabbit infected with rabies has been studied by NELIS. He holds that the organ is not visible in the normal nerve cells of mammals, but that it is brought into plain view during chromatolysis which accompanies rabies. He suggests that this reappearance of the centrosome immediately before the nucleus atrophies indicates a tendency toward cell division at that

time. Such a hypothesis is supported also by the fact, observed by several investigators, that karyokinetic figures occur in the nerve cells of animals infected with rabies.

HATAI, however, finds the centrosome present in the nerve cell of the adult rat, though it is not so generally found in the adult as in the young. The centrosphere is here densely surrounded with neurosomes which go out in radial lines from it, somewhat as KOLSTER finds in *Petromyzon*. Within the clear centrosphere HATAI finds, also, radii of extremely fine granules centering in the centrosome and staining like it. In some cases the place of the single centrosome may be taken by a number of smaller granules, but in such cases the radial arrangement in the centrosphere is lost. HATAI ('02) describes also the behavior of the centrosome in the mitosis in the embryonic nerve cell. One of the two centrosomes seems to migrate to the opposite pole of the nucleus and then each divides, giving two centrosomes in each centrosphere during the mitotic process.

The Tigroid Substance and Chromatolysis.

I. Structural and Chemical Features.—The studies of SCOTT ('99) upon the chemistry of the tigroid substance of the nerve cell are especially noteworthy since they are based upon both embryological and comparative methods, and since he has employed both cytological and micro-chemical technique. He has not confined himself to the use of the NISSL method, but has used toluidin blue and eosin to differentiate the oxyphile and the basophile substances.

By the haematoxylin method for the Prussian blue reaction after treatment of the tissue with acid ferrocyanide, and by the ferrous sulphide reaction after treatment with ammonium sulphide and glycerine, the basophile and oxyphile nuclear substance and the tigroid bodies show the presence of iron. By the oxide of molybdenum reaction after treatment with a nitric acid solution of ammonium molybdate followed by phenylhydrazin hydrochloride the same elements of the cell show the presence of phosphorus. In digestive tests SCOTT finds that immersion for several days in 0.2 per cent hydrochloric acid, at 37°C., does not affect the oxyphile nuclear substance, but after digestion in pepsin and hydrochloric acid the oxyphile substance cannot be demonstrated by the most vigorous stains. In the pepsin experiments the nucleolus sometimes disappears, but SCOTT considers that it is only loosened from the slide by the digestion of its oxyphile center by which it may have been attached.

While treatment of the nerve cell with acid alcohol aids in dem-

onstrating the presence of iron, prolonged treatment will extract all the iron and render the tissue colorless under the toluidin blue stain. Yet after all the iron has been extracted phosphorus is still demonstrable in the tigroid substance and in the oxyphile and basophile nuclear substance. Treatment with alkalis removes the iron from the tigroid substance but not from the nucleolus and the oxyphile nuclear substance, excepting when the treatment is prolonged, while the nuclei of neuroglia cells in the same preparations stain normally in eosin and toluidin blue. Prolonged treatment in the alkalis, however, does not affect the phosphorus of the cell. The author finds that fresh defibrinated ox-blood, owing to its alkalinity, has the same effect as potash of soda upon the nerve cells fixed in alcohol.

By these differential methods SCOTT concludes that the tigroid substance is one of at least three nuclein compounds found in the nerve cell, the other two being the "basophile covering of the nucleolus and the oxyphile nuclear substance." The descent of the three compounds was traced by SCOTT from the chromatin of the germinal cell. "The chromatin," he says, "divides into two parts, each containing iron and phosphorus, but the one is oxyphile and remains in the nucleus, while the other is basophile and diffuses into the cell body and becomes the NISSL granules." This position would seem to be supported, also, by VAN GEHUCHTEN ('97) who is inclined to think that the nuclein (chromatin) of the karyochrome cell is equivalent to the chromatin substance of the somatochrome cell.

If the nuclear chromatin is the source of the first chromatic elements in the cytoplasm of the embryonic nerve cell, does it continue this role in the adult cell? If it does, in what manner is the distribution of the chromatic elements from the nucleus to the cytoplasm brought about?

HOLMGREN ('99) has described an elaborate process, which we have discussed in the section relating to the nucleus, by which the nuclear wall breaks down and the oxyphile nuclear substance migrates into the cytoplasm and becomes at the same time metamorphosed into basophile tigroid substance. By the same process also the basophile covering of the nucleolus breaks off in large masses which are carried out into the cytoplasm. SCOTT, however, since he considers that the breaking down of the nuclear membrane and the displacement of the nucleolus is an artifact, is convinced that, if the transference of chromatic substance from the nucleus to the cytoplasm continues during adult life, the process is diffusion and in no sense a transposition of formed chromatic bodies. However, the nuclear origin of the tigroid

substance, at least in the adult, is opposed by VAN DURME, who believes that the tigroid substance is derived from the nucleo-albumins of the lymphocytes.

VAN GEUCHTEN ('97), accepting the reticular structure of the ground substance, believes that the tigroid substance accumulates at the nodal points of the net. These accumulations enlarge in certain regions and form masses which appear homogeneous when they become sufficiently dense to obscure the reticular framework. A mesh of the reticulum which remains unfilled produces a vacuole. VAN GEUCHTEN attributes the formation of these bodies to the affinity of the protoplasmic net for a special chemical substance. It is, therefore, the form and disposition of the cytoplasmic net that determines the size and distribution of the tigroid bodies; and this, in turn, is governed by the function of the neurone.

SCOTT ('99), on the contrary, argues that the shape and distribution of the tigroid bodies are determined by the modification in the shape of the cell during growth. The tigroid substance diffusely permeates the whole cytoplasm in the early history of the cell. But the growth of the cell and especially the development of the protoplasmic processes break the substance up, by a purely mechanical process, into separate bodies. The distribution of these bodies would seem, therefore, to be governed by the proportions and shape assumed by the cell.

SCOTT takes the position, furthermore, that the tigroid substance cannot be considered as a part of the cytoplasmic net since it diffuses into the cytoplasm after the net is formed. Though the two substances may be intimately associated, they are structurally distinct. He considers that the granules are homogeneous and that appearances to the contrary, including vacuoles, are to be explained by irregularities in their surfaces.

In *Lophius* HOLMGREN ('99) finds that the tigroid body may be resolved into two constituents: a homogeneous ground substance, which stains bluish gray in iron haematoxylin and which tends to stain in both colors with toluidin-erythrosin; and granules which are suspended in the ground substance and which stain black in iron haematoxylin and deep blue in toluidin-erythrosin. The ground substance forms in areas of varying shape and size and the granules may be diffusely distributed through it or massed into solid bodies of different proportions. HOLMGREN does not discover any definite relation of these bodies to a formed ground substance of the cytoplasm.

Although the substance occurs in comparatively small amounts in

the nerve cells of *Lophius*, HOLMGREN describes an interesting feature of its distribution in the cell. Its ground substance has a two-fold arrangement relative to the centrosome; in radii which widen as they approach the periphery of the cell, and in concentric circles around the centrosome. Both the radial and circular bands are more or less irregular in outline. This typical arrangement, however, is often found modified or obscured. The circular bands may overlap each other and those which come nearest the nucleus are more or less diverted from their symmetrical course so as to encircle the nucleus. And on the side of the nucleus nearest the centrosome the tigroid substance collects into a mass of unusual size and becomes involved in the process of transfusion of nuclear substance into the cytoplasm as we have described in the section relating to the nucleus.

HOLMGREN ('00) believes that the distribution of the tigroid bodies is determined by the arrangement of the canaliculi. He has noticed that the tigroid substance of a given cell is most abundant in the region of the most conspicuous canaliculi; also, that it is very abundant in the nerve cells of animals which are characterized by numerous canaliculi. Furthermore, electrical stimulation of the nerve cell is accompanied by an increase in the tigroid substance and also by an expansion of the canaliculi.

Although HOLMGREN's interpretation regarding the increase in tigroid substance under electrical stimulation of the nerve is open to serious objection, his observation would nevertheless support his thesis that the condition of the tigroid substance is correlated with that of the canaliculi. This idea received further support from the observations of PUGNAT ('01) who finds that the canaliculi appear synchronously with the tigroid bodies in the embryonic nerve cell of the chick.

Regarding the function of the tigroid substance, its relation to the ground substance and its embryogenesis point to the same conclusion: that it is a nucleoproteid whose kinetic energy is transformed into potential energy by the metabolism of the cell. The distribution of the substance through the cytoplasm may, as SCOTT points out, contribute to a more prompt and rapid metabolism than if the activities were restricted to the nucleoproteids within the nucleus. This interpretation seems to be born out further by the facts of chromatolysis.

II. Chromatolysis.—In the strict sense "chromatolysis" applies only to a progressive diminution of the chromatic substance of the cell, but other phenomena which seem to be concomitant with this change will be, for convenience, included in this discussion.

VAN DURME ('01) has studied with the NISSL method the PURKINJE cells and the cells of the cerebral cortex of the rabbit under conditions of rest, fatigue and exhaustion. In the cerebellum of the normal specimen at rest he finds cells of two types: "chromophiles," with relatively large amount of chromatin; and "chromophobes," with relatively small amount of chromatin. Both types vary greatly in size. In the chromophiles the protoplasm is uniformly blue with sharply colored chromatic bodies of various form and size. The larger ones lie near the nucleus and a crescent of chromatic substance rests upon the side of the nucleus. The nucleus is of oval form and the karyoplasm stains uniformly blue. Nissl bodies occur also in the proximal portion of the axone. The reticular structure of the cytoplasm cannot be seen. In the chromophobes, however, the cytoplasmic reticulum is apparent, while the cell body is on the average larger than the chromophiles. The peripheral zone is in many cases comparatively free from chromatic substance and the axone is entirely free from it.

Whether these two types are actual or due to functional conditions VAN DURME is not positive, for, as he points out, it is impossible to find all the cells of the nervous system in a condition of absolute rest. He finds, accordingly, that in rabbits which have been killed in the early morning there is great variation in the proportion of the two types of cells.

For studying the condition of the cerebral and cerebellar cells during activity and fatigue VAN DURME stimulated these regions indirectly through the spinal cord with electricity. He examined the cerebrum and cerebellum after continuous stimulation of the cord for periods of five minutes, thirty minutes, two and one-half and seven hours. He concludes from his experiments that abundance of chromatic substance and an oval nucleus are characteristic of the condition of rest. Activity is accompanied by a reduction of chromatic substance in both the cell body and the nucleus, and an increase in volume of the cell body and nucleus. Fatigue, in like manner, is characterized by the presence of cells extremely impoverished of chromatic substance and rich in vacuoles. The author's explanation of this process is noticed in a following paragraph.

Regarding functional changes in the nerve cell of the cerebral cortex, GEERAERD has experimented upon the guinea pig. To produce fatigue he employs natural methods in preference to artificial stimuli such as electricity, which, he believes, is highly objectionable. His argument against it, indeed, seems rational. He recognizes that under natural conditions there is a physiological barrier to over-stimulation

of the central nervous system, but electrical stimulation may drive the central cells beyond the limits of natural activity into morbid processes. From a series of experiments he concludes that activity causes a reduction in size and number of NISSL bodies in the cortical cells, and a diffusion of the chromatic substance into the cytoplasm. There is no noticeable change in the nucleolus. This condition is initial to fatigue and becomes more and more accentuated. Finally the cell, making a last effort, comes into a state of fatigue which is accompanied by increase in volume of the cell body and disappearance of nearly all the chromatic substance of both the cytoplasm and the nucleus.

GEERAERD followed these studies with experiments upon recuperation. By similar methods he examined the cortex of animals which, after complete exhaustion, had been allowed to rest for periods varying from five minutes to an hour. The first indication of repair was discovered after thirty minutes of rest, when the contour of the cell body is found to have regained its normal condition. After three-quarters of an hour a blue zone appears around the nucleolus, which is finely granular with conical projections reaching out to the nuclear membrane. But while the process of repair seems to appear first in the nucleus, the process in the cytoplasm advances from the periphery towards the nucleus. The first tigroid bodies appear next to the cell membrane and gradually invade the deeper regions of the cell. He finds further that while the large pyramidal cells are last to be affected by fatigue they are first to recover.

GEERAERD calls attention to the fact that in the earlier stages of activity the cytoplasm stains a deeper blue than normal but that this is due, not to an increase in the tigroid substance, but to the breaking up into small granules. He believes that this fact accounts for the erroneous position taken by certain authors that activity causes an increase in the tigroid substance.

In comparing the retina of a bird which had been subjected to a bright light for a prolonged period with the retina of another which had been confined for a like period in a dark room, CARLSON ('03) finds there is a "*constant difference in the amount and appearance of the Nissl substance in the cells of the ganglionic and bipolar cell layer.*" The ganglion cells of the stimulated retinae are poorer in NISSL's substance, the NISSL's granules present are less distinct than in the resting retinae, and the protoplasm of the cell bodies takes a diffuse blue stain." This difference is not equally marked in all preparations nor in all regions of the same preparation.

The lesions of the nerve cell accompanying anemia have been

studied by DE BUCK and DE MOOR ('00). Their experiments consisted in an examination of the lumbar cord after temporary and repeated compressions of the abdominal aorta in the rabbit for from five minutes to one hour, and after permanent ligature. They find that following a ligature of one hour no lesion can be discovered if the animal is killed immediately; but if it survive for one hour and a half after the ligature is removed, lesions are apparent. One-half hour is sufficient period of ligature to cause a marked lesion. The chromatic elements break up and ultimately disappear, leaving the cytoplasmic reticulum in view. The nucleus is more resistive than the cytoplasm but finally undergoes homogeneous atrophy. Lesions of this character are more marked in prolonged, continuous ligature than in repeated, temporary ligature. In twenty-four hours after a ligature of an hour many cells were found to be completely destroyed. To all these processes the spinal ganglion cells are more resistant than the cells of the cord. The authors conclude that these changes relating to the cytoplasm cannot be considered as characteristic of anemia, for similar modifications arise from other causes, such as infectious diseases and toxins. The nuclear changes, however, they think, may be characteristic.

VAN GEHUCHTEN's earlier position regarding the lesion of the nerve cell resulting from section of the axone was that all such cases were followed by chromatolysis in the cells of origin. His more recent work ('98), however, leads him to the conclusion that section, or ligature, or a nerve will not always produce chromatolysis in the cells of origin. He observes such a case in the section of the sciatic nerve of the rabbit, in which case the cells of origin are found in the pyknomorphic condition but not in a state of chromatolysis. This condition he attributes to the traumatism. Later researches, in collaboration with VAN BIERVLIET ('00), convince VAN GEHUCHTEN that the lesion of the cell of origin following injury to the nerve varies both according to the intensity of the injury and according to the nerve involved. The cranial nerves appear to be much less resistant than the spinal nerves. The authors conclude also that the cell of origin which is affected by section of the axone may recuperate without regeneration of the axone.

Regarding the comparative cellular lesion which follows mere section of the nerve and extraction of it, DE BEÛLE has experimented upon the rabbit by extracting and sectioning the hypoglossal nerve. The cells of origin were examined at from one to thirty-five days after the operation. He found that on the fourth day the cells were still increasing in size, but on the sixth day they had begun to grow smaller,

though they had not yet returned to the normal size by the tenth day. By the fifteenth day more than half the cells had disappeared, while at the end of thirty-five days there was not a trace of a cell to be found in the position of the nucleus of origin of the affected nerve. The author believes that while, in case of section of a nerve, the cells of origin enter upon a phase of reaction, this is followed by recuperation; but in "arrachment" the phase of reaction is followed by progressive atrophy of the cell.

Following poisoning by arsenic SOUKHANOFF finds that changes of varying intensity appear quickly in the spinal cord and spinal ganglia, and that in many preparations scarcely a normal cell would be found. The lesions of the cell body were marked by diffuse coloration, by loss of regular contour of the chromatic bodies and by turgescence of the cell. More accentuated lesions were characterized by clear spots around the periphery of the cell, owing to the loss of chromatic substance. This was followed by a still more marked lesion expressed by vacuolization of the cytoplasm. The degree of vacuolization varies with the duration of the poisoning. SOUKHANOFF finds no evidence of peripheral chromatolysis which has been described by other authors as characteristic of arsenic poisoning. In the nucleus there appears a diffuse coloration, obscurity of the nuclear membrane and shrinkage.

In his paper upon the finer structure of the nerve cell, VAN GEHUCHTEN ('97) took the position that chromatolysis is essentially a dissolving of the tigroid substance. This results in turgescence of the cell which, beginning at the center, mechanically forces the nucleus towards the periphery of the cell, and causes expansion of the cell. A reconstruction of the chromatic bodies reverses the process. VAN DURME ('01) explains the turgescence of the cell during chromatolysis upon the hypothesis that the katabolic products in the cell, notably sarcolactic acid, increase the osmotic power of the cell and that this produces turgescence.

Chromatolysis itself, VAN GEHUCHTEN ('97) holds, need not be considered as a lesion in the cell. He suggests also, through VAN BIERVLIET ('99), that chromatolysis is, in a sense, a return of the cell to the embryonic condition: that is to say, a condition in which the chromatic substance exists in solution. VAN BIERVLIET also concludes that chromatolysis is perfectly compatible with the normal activities of the cell. DE BEULE ('01) believes that all nerve cells which undergo a non-physiological excitation, which may be traumatic, physical or

chemical, undergo chromatolysis. This is a useful reaction, a utilization of the material to support a special strain upon the cell.

It seems probable, therefore, from the conclusions of these authors, and also from the numerous experiments especially upon poisoning, anemia, and high body temperature, that the nerves may perform their normal function while the cells of origin are undergoing rather marked chromatolysis, and that the cellular lesions resulting from any acute condition may be due in a large measure to general disturbances in the system rather than to the specific disease itself.

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- '97a. Chromatolyse centrale et chromatolyse peripherique. *Travaux*, 1897, Fasc. 2.
- '98. A propos du phénomène de chromatolyse. *Travaux*, 1898, Fasc. 1, pp. 25-34.
- '99. Les phénomènes de réparation dans les cellules nerveux après la section des nerfs périphériques. *Travaux*, 1899, Fasc. 1.
- '00. A propos de l'état moniliforme des neurones. *Le Névraxe*, Vol. I, Fasc. 2, pp. 137-150.

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- '98. La Chromatolyse dans les cornes antérieures de la moelle après désarticulation de la jambe et ses rapports avec les localisations motrices. *Travaux*, 1898, Fasc. 1.

Van Gehuchten, A. and Nelis, Ch.

'98. Quelques points concernant la structure des cellules des ganglions spinaux. *Travaux*, 1898, Fasc. 1, pp. 53-66.

'00. Les lésions histologiques de la rage chez les animaux et chez l'homme. *Le Névrase*, Vol. I, Fasc. 1, pp. 77-114.

Van Gehuchten, A. and van Biervliet, J.

'01. Le noyau l' oculomoteur commun 16, 19 et 21 mois apres resection du nerf. *Le Névrase*, Vol. II, Fasc. 2, pp. 207-216.

LITERARY NOTICES.

Van Gehuchten, A. La dégénérescence dite rétrograde ou dégénérescence Wallérienne indirecte. *Le Névraxe*, Vol. V, Fasc. I, pp. 1-106, April, 1903.

An extensive review of the literature on Wallerian degeneration, followed by experimental studies on degeneration of peripheral and central neurones. The degeneration which occurs between the point of section and the perikaryon is cellulifugal and therefore typically Wallerian. For this phenomenon the author proposes the same "dégénérescence wallérienne indirecte." It occurs in both the central and peripheral systems. In the former, certain fiber tracts undergo only direct degeneration while others undergo both direct and indirect degeneration. The author insists that it must be known exactly which tracts undergo indirect degeneration before the degeneration phenomena can be accepted as trustworthy evidence on certain physiological questions.

G. E. C.

Rossi, Gilberto. Sopra una via efferente encefalo-spinale nell' Emys europaea. *Archivio di Fisiologia*, I, 3, 1904, pp. 332-336.

The forebrain was removed from fifteen turtles and the forebrain and thalamus from fifteen. After about three months degenerated fibers can be demonstrated by VASSALE's modification of MARCHI's method, these being confined to the brain if the forebrain only has been removed, but extending through the whole length of the spinal cord if the thalamus also is removed. This fasciculus thalamo-spinalis is diffusely scattered through the fasc. longitudinalis medialis.

C. J. H.

Langley, J. N. On the Effects of Joining the Cervical Sympathetic Nerve with the Chorda Tympani. *Proc. Roy. Soc.*, LXXIII, No. 489, Feb. 24, 1904.

In this very brief preliminary communication it is mentioned that the cervical sympathetic and the chorda tympani have opposite effects on the blood vessels of the submaxillary gland, the former causing contraction of the vessels and the latter dilation. Two experiments were made

on cats to determine whether the cervical sympathetic, if allowed an opportunity to become connected with the peripheral nerve cells in the course of the chorda tympani, will in part change their function from vaso-constrictor to vaso-dilator. The superior cervical ganglion was excised and the central end of the cervical nerve was joined to the peripheral end of the lingual, which contains the chorda tympani fibers. After allowing time for union and regeneration of the nerves, the cervical sympathetic was stimulated; it caused prompt flushing of the submaxillary glands, and the effect was repeatedly obtained.

The experiment is interpreted as showing (1) that vaso-constrictor nerve fibers are capable of making connection with peripheral vaso-dilator nerve cells and becoming vaso-dilator fibers, and (2) that whether contraction or inhibition of the unstriated muscle of the arteries occurs on nerve stimulation depends upon the mode of nerve ending of the post-ganglionic nerve fiber. The cervical sympathetic gave a less scanty and more prolonged secretion than normal, so that some of its nerve fibers had become connected with the peripheral secretory nerve cells of the chorda tympani.

C. J. H.

Carlson, A. J. The Rate of the Nervous Impulse in the Spinal Cord and in the Vagus and the Hypoglossal Nerves of the California Hagfish (*Bdellotoma dombeyi*). *Amer. Jour. Physiol.*, Vol. 10, pp. 401-418, 1904.

By the use of a graphic method the rate of nerve transmission was determined. Electrical stimulation served to initiate the impulse. In the spinal cord the impulse moves antero-posteriorly, with but slight individual variations, at the rate of 4.50 m. per second. The rate in the opposite direction is 2.50 m. per second, and it is more variable as well as slower than the rate for transmission in the antero-posterior direction. The vagus shows a rate of about 2.50 m., and the mandibular of 4.50 m.

The fibers of the cord as well as those of the peripheral nerves in the hagfish are non-medullated. As the author remarks, this low form of fish has slower transmission in the spinal cord than have certain of the annelid worms in the ventral nerve cord. Furthermore, "the rate in the peripheral motor nerves is the lowest recorded for any vertebrates and even lower than that in the motor nerves of some of the molluscs."

This paper is of value because of its suggestions of possible applications of the reaction-time method in the study of the physiology of the nervous system, as well as for the interesting facts which it presents. Attention is called to evidence in the results of the experiments described "that the rapidity of the processes of conduction in

the nerve stands in direct relation to the rapidity of the process of contraction in the muscle." In the light of this possible relation between the rapidity of muscle contraction and that of nerve transmission the author is led to suggest that "a similar relation may exist between the processes of conduction in the secretory nerves and the processes of secretion in the glands. The rate of the nervous impulse would thus constitute a measure of the relative rapidity of the metabolic process in muscle and gland." As evidence of this relationship the following table seems worthy of reproduction :

Comparison between the contraction-time of the muscle and the rate of propagation of the impulse in the nerve.

Species	Muscle.		Nerve.	
	Muscle.	Contraction-time in seconds.	Nerve.	Rate of the impulse in m.
Frog	gastrocnemius	0.10	sciatic (medullated)	27.00
Snake	hyoglossus	0.15	hypoglossus (medullated)	14.00 ¹
Lobster (<i>Homarus</i>)	flexor of chelae	0.50	first ambulacral (non-medullated)	6.00 ²
Squid (<i>Loligo</i>)	mantle (fin)	0.20	mantle nerve (non-medullated)	4.50 ³
Hagfish	retractor of jaw	0.18	mandibular (non-medullated)	4.50
Hagfish	gill sac	0.45	vagus (non-medullated)	2.50
Octopus	mantle	0.50	pallial (non-medullated)	2.00 ³
Slug (<i>Limax</i>)	foot	4.00	pedal (non-medullated)	1.25 ³
Sea Hare (<i>Pleurobranchaea</i>)	foot	10.00	pedal (non-medullated)	0.75 ³
Slug (<i>Ariolimax</i>)	foot	20.00	pedal (non-medullated)	0.40 ³

¹ **Carlson.** *Archiv für die gesammte Physiologie*, ci, p. 23, 1904.

² **Fredericq and Vandeveld.** *Bulletins de l'Académie Royale du Belgique.*

³ **Jenkins and Carlson.** *American Journal of Physiology*, viii, p. 251, 1903.

R. M. Y.

Carlson, A. J. Beiträge zur Physiologie der Nervensystems der Schlangen.
Pflüger's Archiv, Bd. 101, pp. 23-51, 1904.

This paper is a report of an experimental study of the physiology of the snake. Its results include (1) certain functional indications of the nature and courses of the nerve tracts in the cord, (2) the determination of the rate of nerve impulse, it being in the cord 16 m. per

second (for the centrifugal), and in the hypoglossus nerve 10.5 m. per second, (3) observation that the brain is able to execute apparently conscious functions at least two and a half hours after separation from the spinal cord.

R. M. Y.

Kiesow, F. Contribution à l'étude de la vélocité de propagation du stimulus dans le nerf sensitif de l'homme. *Archives Italiennes de Biologie*, t. 40, pp. 273-280, 1903.

By carefully measuring the reaction-time of thoroughly trained subjects to tactual stimuli applied at different regions of the arm or leg KIESOW has succeeded in showing to his satisfaction that the rate of transmission in the sensory nerves of man is practically the same as for the motor nerves, 30 to 33 m. per second.

The work is very clean cut, and the results are so uniform that one cannot doubt the truth of the author's conclusions. R. M. Y.

Motora, Yujiro. A Study on the Conductivity of the Nervous System. *Amer. Jour. Psy.*, Vol. 14, pp. 329-350, 1903.

This is a brief discussion of theories of nerve conduction, and a description of certain experiments upon which the author bases his so-called hydraulic theory.

For the facts of nerve transmission, he writes: "I propose an hydraulic explanation. It supposes that nervous conduction is a transmission of a water wave in a protoplasmic tube and that the protoplasmic tube not only helps the transmission by its own elasticity but is excitable at any point by means of a stimulus directly applied to it."

MOTORA experimented with water-filled tubes under various conditions to determine whether the phenomena characteristic of nerve conduction are exhibited also by them. The experiments deal with the following topics: Experiment 1—Rate of transmission of water wave in rubber tubes. It was found to be about 100 feet per second, or approximately the same as the nerve rate. Experiment 2—Evidence of an action current. Under certain conditions, we are told, the wave in a tube filled with slightly acidulated water is accompanied by what appears to be a thermo-electric current. The author writes concerning the action current in the nerve, "I believe that the action current is explicable as a thermo-electric current produced between two points of the nerve where the electrodes touch it." Experiment 3—Inhibition phenomena. This study of the interference of water waves leads the author to the conclusion that the phenomena of attention and inhibition "are very conveniently explained under the supposition of a protoplasmic tube" (filled with fluid).

Although the paper yields no definite results so far as our knowledge of the nature of the nerve impulse is concerned, it contributes several curiously interesting facts, and a few analogies of problematic value.

R. M. Y.

Lillie, Ralph S. The Relation of Ions to Ciliary Movement. *Amer. Jour. Physiol.*, Vol. 10, pp. 419-443, 1904.

Gowers, William R. Subjective Sensations of Sight and Sound, Abiotrophy, and other Lectures. *Philadelphia, P. Blakiston's Sons & Co.*, 1904.

This is a collection of lectures mostly published before, but well worth having united in book-form, and carefully revised.

The lecture on subjective visual sensations limits itself largely to the conditions in migraine, epilepsy; the one on subjective sensations of sound to the various forms of tinnitus. As such they form an interesting supplement to any chapter of hallucinations. A note (p. 90-95) is a plea to change the accepted form of designating musical notes as C_3 C_2 C_1 C^1 C^2 C^3 C^4 C^5 C^6 , which gives the "neutral C" to the middle C between the bass and treble staves, and has some mnemotechnical advantages concerning the number of vibrations ($C_3=33$; $C_2=66$; further C^1 the first number with four figures, i. e. 1065, and $C^4=4224$).

The lecture on Abiotrophy; (diseases from defect of life) introduces a new term for deficiency of vitality of special tissues and parts of tissues: skin, baldness, muscles, nervous system, etc., and the supplementary interstitial overgrowth, either as deficient constitutional endowment, or as such defect brought on through toxic and toxic factors with selective degenerations. Lecture IV, on Myopathy and a Distal Form, deals with an important type of this group.

The remaining lectures, on Metallic Poisoning, Syphilitic Diseases of the Nervous System, Inevitable Failure (a study of syphilitic arterial disease), Syringal Haemorrhage into the Spinal Cord, Myasthenia and Ophthalmoplegia, and the use of drugs, are probably of more exclusively medical interest.

It is to be regretted that the "Dynamics of Life" are not included in this collection.

A. M.

Bourneville. Recherches et Therapeutiques sur L'Epilepsie, L'Hysterie et L'Idiotie. Vol. 23, *Paris, Félix Alcan*, 1903.

This Annual Report of the Institution at Paris is followed as usual by the study of a number of cases: The Mongolian type (with histological examination of two brains); the rôle of alcoholism in the production of idiocy, etc. This is the 23d Volume of a very creditable series.

A. M.

Raymond, F. and Janet, Pierre. Les Obsessions et la Psychasthénie, Vol. II. *Paris, Felix Alcan, 1903.*

This second volume of the very interesting work of Professor JANET brings the clinical material underlying and further illustrating the discussions of the first volume. It is a treasure of clinical information, full of masterly descriptions and analyses. The whole work is a remarkable continuation of the similar set of two volumes—"Névroses et idées fixes."

A. M.

Mills, Wesley. The Neurones and the Neurone Concept Considered from the Anatomical, Physiological, Pathological and Psychological Point of View. *Montreal Medical Journal*, Dec., 1903.

An illustrated summary of the leading facts on which the neurone doctrine is based, occupying 22 pages.

C. J. H.

Dogiel, A. S. Ueber die Nervenendapparate in der Haut des Menschen. *Zeits. f. w. Zool.*, Bd. 75, H. 1, pp. 46-111, Pl. IV-XIV, 1903.

Methylene blue method. An important histological paper.

J. B. J.

Hübschmann, Paul. Untersuchungen über die Medulla oblongata von *Dasy- pus villosus*. *Zeits. f. w. Zool.*, Bd. 75, H. 2, pp. 258-280, 1903.

J. B. J.

Marengi, Giovanni. Alcune particolarità di struttura e di innervazione della cute dell'*Ammocoetes branchialis*. *Zeits. f. w. Zool.*, Bd. 75, H. 3, pp. 221-429, 1903.

The author finds by the GOLGI method, in addition to the free nerve endings already known, sense cells in the epidermis which give rise to centripetal fibers. The reviewer has studied the same structures, which are frequently impregnated in his preparations of *Lam- petra*, and has come to the conclusion that they are ordinary epider- mal cells, the precipitate upon which is continuous with that upon neighboring free nerve fibers.

J. B. J.

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AN ENUMERATION OF THE MEDULLATED NERVE FIBERS IN THE VENTRAL ROOTS OF THE SPINAL NERVES OF MAN.

By CHARLES E. INGBERT.

(From the Neurological Laboratory of the University of Chicago).

With 38 Figures in the Text.

- I. *Introduction.*
- II. *Historical Statement.*
- III. *Determination of the areas of the cross-sections of the ventral roots of the spinal nerves of man.*
 1. KÖLLIKER'S determination.
 2. STILLING'S determination.
 3. Author's determination.
 4. Comparison of areas.
 5. Discussion of Figures 1 and 2.
- IV. *Determination of the number of nerve fibers in the ventral roots of the spinal nerves of man.*
 1. STILLING'S estimate.
 2. Author's enumeration.
 3. Comparison of STILLING'S estimate with the author's enumeration.
 4. Determination of fine nerve fibers.
- V. *The number of nerve fibers per square millimeter of the cross-section of the ventral roots of the spinal nerves of man.*
 1. Determinations and comparisons.
 2. Discussion of Figure 3.
- VI. *Relation between the ventral and dorsal roots.*
 1. Relation of areas of cross-sections.
 2. Relation of the sizes of the nerve-fibers.
 3. Relation of numbers of nerve fibers.
 4. Comparison of the ratio of the number of nerve fibers in the ventral and the dorsal roots of the frog, of the rat, and of man.
 5. Relation of small and large fibers.
- VII. *On the relative area of the cross-section of the roots forming the brachial and lumbo-sacral plexuses in the male and the female.*
- VIII. *Summary.*
- IX. *Tables and figures.*
- X. *Bibliography.*

I. Introduction.

Having completed "The Enumeration of the Medullated Nerve Fibers in Dorsal Roots of the Spinal Nerves of Man" (June, 1903), the author attempted to determine how many of these dorsal root fibers innervated the muscles and other deep tissues, and how many, the skin. For this purpose it was necessary first to determine the number of nerve fibers in the ventral roots. This was done. Using the number obtained in this enumeration, an estimate was made "On the Density of the Cutaneous Innervation in Man" (October, 1903).

The purpose of this present paper is to give in detail the results obtained from the study of the number of fibers in the ventral roots.

II. Historical Statement.

Although estimations of the number of medullated nerve fibers in different spinal and cerebral nerves of man and determinations of the areas of their cross-sections have been made by D. ROSENTHAL (1845), STILLING (1859), TERGAST (1872), KUHN (1879), W. KRAUSE (1876 and 1880), SALZER (1880), and VOISCHVILLO (1883), no complete count of the spinal nerves had been made prior to the author's observations cited above (June, 1903). We are now able to add a similar enumeration of the medullated nerve fibers in the ventral roots of the spinal nerves of the same man. For a description of the material, the reader is referred to the paper first mentioned above.

III. Determination of the Areas of the Cross-Sections of the Ventral Roots of the Spinal Nerves of Man.

1. *Kölliker's Determination.*—Under conditions which have been described elsewhere in detail (INGBERT, June, 1903, p. 55), KÖLLIKER (1850, p. 434) determined the area of all the cross-sections of all¹ the ventral roots of the left spinal nerves

¹ KÖLLIKER does not give the areas of the ventral roots of the sacral nerve IV and V. We estimate their combined area as about 0.2 mm² and have corrected his results by adding this amount.

of a man to be (when corrected by adding .2 mm.²) 34.51 mm².

2. *Stilling's Determination.*—In the paper just referred to (INGBERT, June, 1903, p. 55) the details of the conditions under which STILLING (1859, p. 346) made his measurements are also given. His determination for the total area of all the ventral roots of the left spinal nerves in a woman was 35.23 mm².

3. *Author's Determination.*—Using a method similar to that employed in the measuring of the areas of the dorsal roots (INGBERT, June, 1903, p. 56), it was found that the total area of the ventral roots of the left spinal nerves of the same individual amounted to 26.50 mm².

4. *Comparison of Areas.*—The total areas of the cross-sections of the ventral roots of the left spinal nerves obtained by the preceding investigations are as follows :

KÖLLIKER (male)	34.51 mm ²
STILLING (female)	35.23 mm ²
Author's Case (male)	26.50 mm ²

As the case here presented shows a smaller area than that found by either KÖLLIKER or STILLING some comment is called for. It may be stated at the outset that the areas for the ventral roots in the author's case were measured in 365 distinct fascicles; that, further, from the total area first determined in this way there was ultimately subtracted 1.54 mm², representing the excess of area caused by fascicles cut obliquely. In the case of KÖLLIKER's measurements it is readily seen why they should be large, since he included all the connective tissue within the roots in his determination. For example, when the roots in the author's case were measured by the method of KÖLLIKER they gave an area of 40.81 mm². This not only shows why KÖLLIKER's area is large but also indicates that in the particular spinal cord the roots of which he measured, the roots themselves were rather small. This conclusion is supported by the fact that STILLING, in the case of a woman, found the area of the left ventral roots to be 35.23 mm². Yet STILLING measured the roots in fascicles, by means of a planimeter, and thus included much less connective tissue than KÖLLIKER. That STILLING's result is larger than that of the author might be ex-

plained in part by the fact that he divided the roots into a smaller number of fascicles (211 against 365) and that he did not correct for the fascicles cut obliquely. At the same time it seems necessary to assume that the ventral nerves in STILL-

TABLE I.

Areas in sq. mm. of Cross-Sections of the Ventral Roots of the Left Spinal Nerves of Man.

	No. of Spinal Nerve.	Average length of Segments in mm. according to DONALDSON and DAVIS, 1903.	KÖLLIKER	INGBERT	STILLING
			Male	Male	Female
Cervical	I	7.2	1.00	.25	.63
	II	9.7	1.21	.69	1.32
	III	12.4	.81	.31	.77
	IV	14.3	.55	.84	1.02
	V	12.4	1.74	2.81	2.78
	VI	13.8	1.79	2.69	2.56
	VII	12.9	2.82	1.22	2.10
	VIII	13.2	1.79	1.52	1.81
Thoracic	I	12.8	1.00	.76	1.15
	II	14.2	.55	.45	.51
	III	17.3	.58	.53	.48
	IV	20.9	.64	.44	.57
	V	21.9	.49	.53	.66
	VI	23.6	.92	.52	.53
	VII	24.2	.92	.46	.58
	VIII	25.1	.92	.49	.63
	IX	23.5	.88	.49	.74
	X	22.5	.77	.58	.68
	XI	21.4	1.00	.57	.49
	XII	19.6	.92	.60	.56
Lumbar	I	18.3	.92	.66	.63
	II	12.9	1.04	.81	.70
	III	11.8	2.43	1.87	1.55
	IV	10.6	1.96	1.27	2.69
	V	8.2	1.96	2.17	2.06
Sacral	I	7.7	2.82	1.98	2.68
	II	8.4	1.59	.61	2.75
	III	7.1	.25	.17	1.15
	IV	6.7	{ .20 ¹	.10	.33
	V	4.8		.09	.10
Coc.	I	2.5	.04	.02	.02
Totals	31	441.9 mm.	34.51 mm ² .	26.50 mm ²	35.23 mm ²

¹ Interpolated.

the curves for the areas of the dorsal roots (INGBERT, June, 1903, p. 61).

5. *Discussion of Figs. 1 and 2.*—The three curves in Fig. 1 are based on the absolute areas of the cross-sections of the ventral roots of the left spinal nerves, and show a general similarity. Thus, they all show C. III smaller than C. II. A marked elevation for the roots innervating the muscles of the limbs and a depression for the thoracic roots is evident: Yet individual roots may vary considerably in area. In KÖLLIKER'S curve the largest cervical root is C. VII, a root considerably diminished in the author's curve and in STILLING'S. Again, C. V is large in STILLING'S and author's curves, but not so in KÖLLIKER'S. In all, there seems to be a tendency to a depression at C. VI. The interesting fact in connection with these points is that C. V-VI correspond roughly to the roots innervating the muscles of the shoulder and upper arm, and C. VII to the intrinsic muscles of the hand. In the lumbar region attention is called to the position of the curve between L. III and S. II, which exhibits two elevations bounding an intervening depression represented by one or two roots. In the curve from the author's data the first elevation is at L. III, and the second at L. V, with L. IV depressed. Here L. III represents the root partly innervating the main flexors of the leg and foot. It is also evident that the largest root in the cervical or lumbar regions may be shifted one or more segments cephalad or caudad from an intermediate position. The three curves in Fig. 2 are based on the areas represented as percentages of the largest root in each series. The discussion of Fig. 1 applies to this figure also.

IV. Determination of the Number of Nerve Fibers in the Ventral Roots of the Left Spinal Nerves of Man.

As the study of the number of nerve fibers in the ventral roots was carried on in a manner similar to that used for the dorsal roots, the reader is referred to the preceding paper (INGBERT, June, 1903, pp. 62-67) for a general statement of the technique and sources of error. Certain specific statements,

however, require to be made concerning the ventral roots, and these will be given as briefly as possible.

1. *Stilling's Estimate.*—STILLING (1859, p. 600) counted in a series of squares 1-156 of a square line in area, the number of cross-sectioned nerve fibers seen within them, and from this estimated the the number for an entire square line.¹ This he found to be from 120 to 156, average 138, for the ventral roots. He does not state what roots he examined, nor how many counts were made. If 1-156 of a square line of the section contains 138 fibers, one square line will contain 156×138 , or 21,528 fibers, which is equal to 4231 fibers for each square millimeter. Since in his case there were 35.23 mm^2 in the area of the ventral roots of the 31 left spinal nerves, there will be 35.23×4231 , or 149,058 nerve fibers in all of them. And since the right ventral roots were found to have an area of 37.17 mm^2 they will have $37.13 \times 4,231$ or 157,266 nerve fibers, and the ventral roots of both sides, 306,324.

STILLING's estimate for the number of nerve fibers in the ventral roots of both sides is, however, not 306,324 but 303,265. This difference is due to the fact that he based his final estimate on the area of ventral roots as obtained by his method of weighing, which gave 71.697 mm^2 for both sides, and the calculations I have made are based on his areas as obtained by the planimeter, which give 72.40 mm^2 . The latter areas were selected because they may be more properly compared with my own, which were also obtained by planimetric measurements.

2. *Author's Enumeration.*—By the methods and under the conditions referred to in the earlier paper there were found in all ventral roots of the spinal nerves of the left side 203,700 nerve fibers. The details of this enumeration are given in the accompanying Table II.

In Tables VIII-XXXVIII are to be found the numbers of nerve fibers for each fascicle, and in Table II are found the totals for each root.

¹ STILLING used the Paris line, the value of which is 2.2558 mm.

TABLE II.

Showing the Number of Nerve-Fibers Counted in the Ventral Roots of the Left Spinal Nerves of Man.

		No. of spinal nerve.	Area of roots in sq. mm.	No. of nerve fibers in each root.	No. of nerve fibers, in thousands, per sq. mm.
Cervical	I		.25	3,406	13.4
	II		.69	4,259	6.2
	III		.31	3,850	12.3
	IV		.84	5,955	7.1
	V		2.81	13,548	4.8
	VI		2.69	11,794	4.4
	VII		1.22	8,913	7.3
	VIII		1.52	8,435	5.5
Thoracic	I		.76	7,276	9.5
	II		.45	5,625	12.6
	III		.53	7,235	13.5
	IV		.44	7,625	17.2
	V		.53	6,736	12.7
	VI		.52	6,298	12.2
	VII		.46	5,655	12.2
	VIII		.49	6,074	12.5
	IX		.49	5,789	11.9
	X		.58	7,171	12.3
	XI		.57	7,761	13.7
	XII		.60	7,596	12.9
Lumbar	I		.66	7,944	11.9
	II		.81	6,014	7.4
	III		1.87	11,138	5.9
	IV		1.27	7,349	5.8
	V		2.17	10,366	4.8
Sacral	I		1.98	8,598	4.3
	II		.61	4,406	7.2
	III		.17	2,340	13.5
	IV		.10	2,323	23.9
	V		.09	1,702	19.0
Coc.	I		.02	519	30.0
31			26.50 mm ²	203,700	7.7

In Table II attention is called to the following points :

1. The total number of fibers in the ventral roots of the left side is 203,700.
2. The small root C. III has 3,850 fibers.
3. The large roots C. V-VI—innervating in part the muscles of the shoulder and flexors of the upper arm.

4. The uniformity of the number of fibers in the thoracic roots.
5. The number of fibers in the largest cervical root, which is twice the average number in the thoracic roots.
6. The large roots in the lumbo-sacral region—L. III—innervating in part the adductors and flexors of the thigh; and L. V—innervating in part the flexors of leg and foot.
7. The depression at L. IV—corresponding to the demarcation between the lumbar and the sacral plexuses.
8. In this case—a male—the four largest cervical roots (C. V, VI, VII, VIII) contain more fibers than the four largest successive lumbo-sacral roots (L. III, IV, V and S. I.)
9. That the number of nerve-fibers per sq. mm. of the cross-section of the ventral roots shows that the fibers in the roots passing to the brachial and the lumbo-sacral plexuses have an average diameter which is large, and that the fibers in the thoracic roots have an average diameter which is small.

3. *Comparison of Stilling's Estimate with the Author's Enumeration.*—The determinations of the number of medullated nerve fibers in the ventral roots of the left spinal nerves of man in the case which we have just discussed, give the following result:

Author's Enumeration 203,700 nerve fibers.

This result shows that STILLING'S estimate, 149,057, is 73.17% of the author's enumeration, or, in other words, the author's result is 26.83% greater than STILLING'S. On searching for the cause of this difference, we find two significant statements made by STILLING. First, he says that he did not observe in either the ventral or the dorsal spinal roots (at least not in the material fixed in chromic acid), nerve fibers of such diameters as KÖLLIKER reports (2.7 to 4.5 μ); and secondly, that the diameters of the medullated nerve fibers in the ventral roots range from 7.5 to 22.5 μ (STILLING, 1859, p. 678). It is thus evident that one source of difference between STILLING'S esti-

mate and my own is the fact that STILLING's estimate does not include the nerve fibers, the diameter of which is less than 7.5μ .

As we have already noticed, my results are 26.83% greater than STILLING's. The question, therefore, is to what extent this difference can be accounted for by the nerve fibers in the ventral roots, the diameter of which is less than 7.5μ .

KÖLLIKER (1850) makes the statement that in the ventral roots three-fourths of the fibers range from 13.5 to 24.9μ , and the small fibers are for the most part from 5.6μ to 6.8μ .

To determine the relation between the fine and the large fibers in the ventral roots of man, SIEMERLING (1886-'87) counted in each root, mostly on the left side, the nerve fibers seen in 9 sq. mm. of the ocular micrometer (oculus 3, system 7, HARTNACK). He thus counted in the ventral roots 559 fibers, the diameter of which was less than 7.5μ and 552, the diameter of which was more than 7.5μ .

In other words, the fine and large fibers were found by him to be about equal in number.

Such a small count as this must be considered, however, very inadequate in the determination of a relation, subject to such considerable local variations.

4. *Determination of the Fine Fibers in the Ventral Roots.*—

To determine this point, the author has made counts from a few fascicles of each of the ventral roots of the spinal nerves. In making these counts, such fascicles were selected as had the same number of nerve fibers per square mm. of the cross-section as the average found for the entire root. The fibers, the diameter of which was 7.5μ or more were considered large fibers, and those the diameter of which was less than 7.5μ were considered small fibers. After finding what per cent of the selected fascicles was represented by small fibers, the number of small fibers in the entire root was calculated in accordance with this relation.

The results are presented in Table III.

According to the calculations in this Table there are in the ventral roots 80,747 nerve fibers the diameter of which is less

than 7.5μ . Since there are in all 203,700 nerve fibers in the ventral roots of the left spinal nerves and of these 80,747 are small fibers, it appears that the small fibers constitute 39.64%

TABLE III.

Showing counts made in the different ventral roots in order to determine the relation between the number of large fibers (7.5μ or more in diameter), and the number of small fibers (less than 7.5μ in diameter).

Root	No. of Fasc. See Figs. 8-28.	No. of fibers	No. of large fibers	Large fibers in %	Small fibers in %	Calculated small fibers in entire root.	
Cervical	I	15, 17	310	246	79	21	715
	II	2, 3, 12	1522	1303	86	14	468
	III	9, 18	736	571	78	22	847
	IV	9	412	351	85	15	893
	V	19, 26	731	929	86	14	897
	VI	4, 16, 19	1057	936	88	12	1415
	VII	19	912	786	86	14	1248
	VIII	4	407	366	90	10	844
Thoracic	I	7	857	472	55	45	3274
	II	2	803	370	46	54	3038
	III	All	7235	1964	27	73	5271
	IV	All	7625	1786	24	76	5839
	V	10, 12	1565	385	25	75	5062
	VI	3, 5	1785	541	30	70	4409
	VII	All	5655	1875	33	67	3780
	VIII	3	2182	820	38	62	3766
	IX	4	598	211	35	65	3703
	X	11	1047	318	30	70	5020
	XI	2, 3	913	246	27	73	5066
	XII	2, 4	1176	333	29	71	5393
Lumbar	I	1	264	84	32	68	5302
	II	3, 5	1050	859	82	18	1083
	III	9, 10, 16	1375	1246	91	9	1003
	IV	11, 7, 13	1762	1520	87	13	955
	V	7, 9, 11	3405	2877	85	15	1555
Sacral	I	5, 8	1327	1134	86	14	1204
	II	8	568	300	69	31	1366
	III	1, 2	2340	690	30	70	1038
	IV	All	2323	258	11	89	2067
	V	All	1702	322	11	89	1380
Coc.	I	1	510	33	6	94	486
Total 80747							

NOTE—The numbers marked by a star * do not represent the fibers counted, but were obtained by subtracting the small fibers which were counted in these fascicles from the entire number of fibers in the fascicle.

of the entire number. We have already stated that the author's enumeration of the nerve fibers in the ventral roots of the left spinal nerve is 26.83% greater than the estimate made by STILLING. And we have also shown that STILLING failed to include in his estimate the nerve fibers the diameter of which is less than 7.5μ . It therefore seems probable that these small fibers would account for the difference (26.83%) between the author's enumeration and STILLING's estimate. Were this exactly the case, the small fibers should amount to about 26.83% of the entire number in the ventral roots. But we have found that the calculation made above places the small fibers at 39.64%. It therefore becomes necessary to search for the cause of this discrepancy. The above reasoning, (i. e., that the percentage of small fibers should exactly account for the difference) is valid only on the assumption that the number of large fibers was similar in the two cases compared. We must therefore determine whether or not the ventral roots used by STILLING probably contained the same number of large fibers as the ventral roots used by the author. To simplify this matter we shall again compare the areas of the ventral and dorsal roots of the left spinal nerves, as determined by STILLING and by the author.

	Total area of ventral roots	Total area of dorsal roots	Ratio
STILLING (female)	35.23 mm. ²	57.95 mm. ²	1:1.64
Author (male)	26.50 "	54.93 "	1:2.07

We have already suggested that the ventral roots in STILLING's case were larger than we should expect and the table above illustrates this point. Taking the areas of the dorsal roots as standards and assuming our own area for the ventral roots to be correct, then the following proportion (54.93 : 57.95 :: 26.50 : x) gives 27.96 mm.² as the area to be anticipated for the ventral roots in STILLING's case. From this it is evident that if we could assume the same ratio to exist between the ventral and dorsal roots in males and females, the area of the ventral roots in STILLING's case should be 27.96 mm.² instead of 35.23 mm.². We have here, probably, the reason for the discrepancy between the number of fibers by which the

author's enumeration differs from STILLING's estimate (26.83%) and the number of small fibers actually found (39.64%).

To test this, another calculation becomes necessary. The ventral roots of the left spinal nerves, according to STILLING, have an area of 35.23 mm.² and contain 149,058 nerve fibers. If these ventral roots had an area of only 27.96 mm.², their area would be in the same ratio to the area of the dorsal roots as are the areas in the author's case, and would contain (according to STILLING's method of estimation) only 118,299 nerve fibers. This is 58.07% of the author's estimation; or, in other words, it is 41.93% less. But from our calculation above the small fibers in the author's case constitute 39.64%, hence we conclude that the difference between STILLING's estimate of the number of nerve fibers in the ventral roots and the author's enumeration is accounted for within 2% by the small fibers which STILLING omitted. It does not seem probable that this increased area in the ventral roots in STILLING's case was due to large masses of connective tissue for he was on his guard against this source of error; but a diffused increase might have been present.

Finally, the difference may be due to individual variation, or may be due to difference in sex. This later possibility will be considered further on.

V. The Number of Nerve Fibers per Square Millimeter in the Cross-Sections of the Ventral Roots of the Left Spinal Nerves of Man.

1. *Determinations and Comparisons.*—According to STILLING, the ventral roots of the left spinal nerves have an area in cross-section of 35.23 mm.² and contain 149,058 medullated nerve fibers, or, in other words, they contain 4,231 nerve fibers per sq. mm. of the cross-section.

According to the author's results, the ventral roots of the left spinal nerves have an area in cross-section of 26.50 mm.², and contain 203,700 medullated nerve fibers, or, 7,687 nerve fibers per sq. mm. of their cross-section.

The difference between the number of nerve fibers sq. mm.

obtained by STILLING and that obtained by the author, has the same explanation as the difference in the total number of fibers—STILLING did not include the fibers, the diameter of which was less than 7.5μ , and at the same time, for some reason not yet apparent, his areas are large.

In Tables VIII-XXXVIII and Figures 8-38, are given the number of fibers per sq. mm. in each fascicle expressed in thousands. A study of these shows that great variations may occur in the neighboring roots, and even in fascicles of the same root. The small number per sq. mm. in the roots forming the brachial and lumbo-sacral plexuses is due to the large fibers in these roots, there being relatively few small fibers in them. The large number per sq. mm. in the thoracic region is due to the very great number of small fibers, many of which, no doubt, pass to the white rami communicantes. The large number per sq. mm. for the root C. III, correlated with the small size of this root, indicates a small diameter for the fibers in this root.

In order to show better the relation between the number of fibers in the roots and the area of the cross-sections of roots, I have constructed, on the basis of the data in Table IV, Fig. 3 (see p. 213). These curves has been drawn in the same manner as the corresponding chart in the author's earlier paper (INGBERT, June, 1903, p. 72).

2. *Discussion of Figure 3.*—In this figure the relative areas of the ventral roots are contrasted with the relative abundance of the fibers in them.

For each series the largest value is taken as 100%, and the other values are calculated on this as a standard. As the root with the largest area (C. V.) is also the root with the largest number of fibers, the two maxima coincide. It is sufficient in this place to call attention to the fact that in the intumescentiae the number of fibers and the area of the roots change in the same manner, so that the two curves are parallel, and that in the thoracic region the number of fibers remains relatively large while the area of the roots is much diminished, thus showing that in these roots the diameter of the fibers is on the average much decreased.

TABLE IV.

Giving the percentage values of the cross-section of the ventral roots of the spinal nerves as compared with the percentage distribution of the number of medullated nerve fibers in each ventral root. The greatest value in each series is taken as 100%.

	No. of spinal nerves	Percentage Value. (INGBERT)	
		Areas	No. of Fibers
Cervical	I	8.9	25.1
	II	24.5	31.3
	III	11.0	28.4
	IV	29.9	43.9
	V	100.0	100.0
	VI	95.7	87.0
	VII	43.4	65.8
	VIII	54.1	62.2
Thoracic	I	27.0	53.6
	II	16.0	41.5
	III	18.9	53.4
	IV	15.7	56.3
	V	18.9	48.2
	VI	18.5	46.5
	VII	16.4	41.7
	VIII	17.4	44.8
	IX	17.4	42.7
	X	20.6	52.9
	XI	20.3	57.3
	XII	21.3	56.0
Lumbar	I	23.5	58.7
	II	28.9	44.4
	III	66.5	82.2
	IV	45.2	54.2
	V	77.2	76.5
Sacral	I	70.5	63.4
	II	21.7	32.5
	III	6.0	17.3
	IV	3.5	16.4
	V	3.2	12.7
Coc.	I	0.7	3.8

VI. *The Relation Between the Ventral and Dorsal Roots.*

1. *Relation of Areas of Cross-sections.*—For comparison we have arranged the areas of the ventral and dorsal roots in tabular form, adding the measurements by KÖLLIKER (1850, p. 433) on the spinal nerves of a female.

Observer	Total area of ventral roots	Total area of dorsal roots	Ratio
KÖLLIKER (male)	34.51 mm. ²	79.74 mm. ²	1:2.31
" (female)	33.48 mm. ²	68.40 mm. ²	1:2.04
STILLING (female)	35.23 mm. ²	57.95 mm. ²	1:1.64
INGBERT (male)	26.50 mm. ²	54.93 mm. ²	1:2.07

The lowest ratio appears in STILLING's case, and the reason for this diminished value is the large area of the ventral roots in his case. The ratio for the author's case (male), 1:2.07, is almost the same as that for KÖLLIKER's (female) 1:2.04.

In order better to compare the relation between the areas of the two series of roots in the case under investigation, Figs. 4 and 6 have been constructed on the basis of data given in Table V (p. 226).

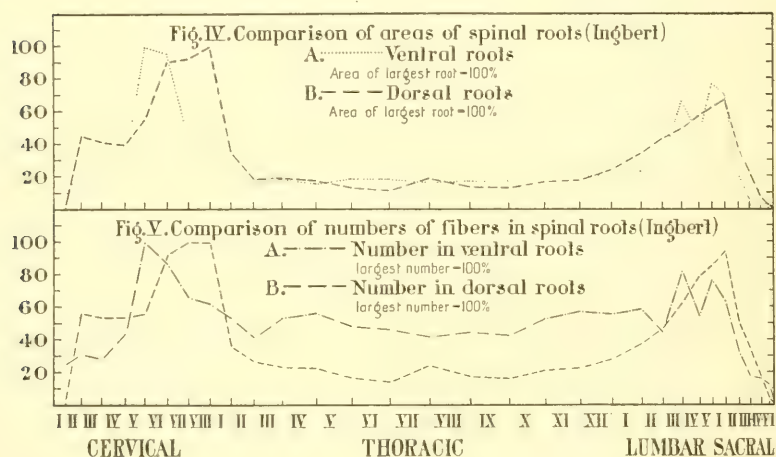


Fig. 4. Curves comparing the area of the ventral and dorsal roots of the left spinal nerves, the values in each curve being entered in percentages of the greatest area, which is taken as 100%. One unit on the axis of the ordinates equals 1%.

Fig. 5. Curves for comparison of the numbers of medullated nerve fibers in the ventral and the dorsal roots of the left spinal nerves. These curves were constructed as those in Fig. 4.

In Fig. 4 is found a comparison between the relative areas of the ventral and dorsal roots of each nerve. In general the two curves are similar—showing that there is the same proportional difference between the large and small ventral roots that occurs between the large and small dorsal roots. The largest ventral roots are located further cephalad in the cord than the largest dorsal roots and this is true for both the cervical and lumbar enlargements.

Moreover, as compared with the curve for the dorsal roots, that for the ventral is distinctly irregular—especially in the intumescenciae.

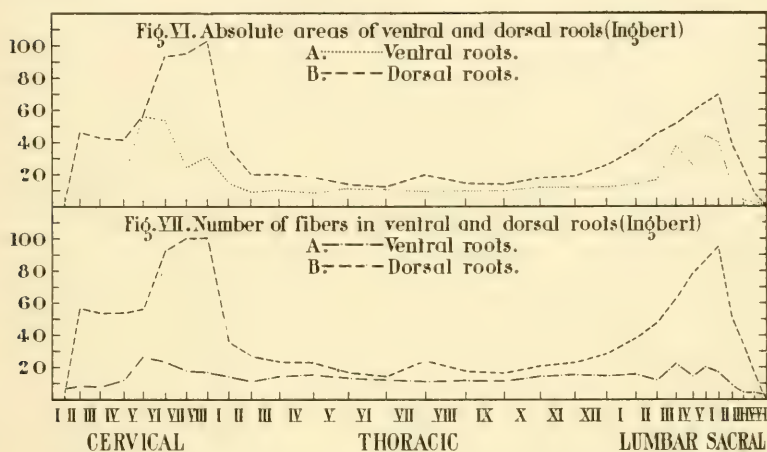


Fig. 6. Curves showing the absolute areas of the cross-sections of the ventral and the dorsal roots of the left spinal nerves. Each sq. mm. is represented by 20 divisions on the axis of ordinates.

Fig. 7. Curves showing the number of medullated nerve fibers in the ventral and the dorsal roots of the left spinal nerves. Each thousand nerve fibers is represented by two units on the axis of ordinates.

The accompanying figure 6 represents the absolute areas of the cross-section of the ventral and dorsal roots. Despite the considerable absolute difference, it has just been shown (Fig. 4) that the relative differences are only slight.

TABLE V.

showing in square millimeters the relation between the absolute areas of the cross-sections of the ventral and dorsal roots.

No. of spinal nerve	Ventral Roots	Dorsal Roots	Ratio
I	.25	.13	1:0.5
II	.65	2.33	1:3.4
III	.31	2.14	1:6.9
IV	.84	2.01	1:2.3
V	2.81	2.82	1:1.0
VI	12.69	4.65	1:1.7
VII	1.22	4.72	1:3.8
VIII	1.52	5.11	1:3.3
I	.76	1.79	1:2.3
II	.45	.97	1:2.1
III	.53	.98	1:1.9
IV	.44	.90	1:2.0
V	.53	.68	1:1.3
VI	.52	.59	1:1.1
VII	.46	.98	1:2.1
VIII	.49	.71	1:1.5
IX	.49	.67	1:1.4
X	.58	.86	1:1.5
XI	.57	.91	1:1.6
XII	.60	1.25	1:2.1
I	.66	1.75	1:2.7
II	.81	2.22	1:2.8
III	1.87	2.52	1:1.3
IV	1.27	2.93	1:2.3
V	2.17	3.20	1:2.4
I	1.98	3.44	1:1.8
II	.61	1.92	1:3.1
III	.17	1.18	1:6.9
IV	.10	.40	1:4.0
V	.09	.13	1:1.4
I	.02	.03	1:1.5
Totals 31	26.50 mm. ²	54.93 mm. ²	1:2.07

2. *Relation of the Size of the Nerve Fibers.*—If the reader will imagine the curve for the area of the dorsal roots (Fig. 6) overlaid by the curve showing the absolute number of fibers in the dorsal roots (Fig. 7) it will be readily seen that the two curves coincide remarkably; the greatest difference occurring in the lumbo-sacral nerves. In an earlier paper (INGBERT, June, 1903, Chart III), these two curves are drawn superposed. The fact that the two nerves run nearly parallel shows that in

general when the area of a dorsal root changes, it is due to a change in the number of nerve fibers composing it, while the average diameter of the fibers remains about the same from root to root. This is also expressed by the fact that the number of thousands of fibers per square millimeter (see INGBERT, June, 1903, p. 67) undergoes but slight variation.

If the corresponding curves for the ventral roots are now examined, some interesting differences between the ventral and dorsal roots at once appear. In the ventral roots (see curves in Figs. 6 and 7) the enlargement of the areas of the cross-sections is not due so much to an increase in the number of fibers in the roots as to the increased diameter of the nerve fibers; hence at the intumescenciae the curve for the areas rises far above the curve for the number of the fibers. In the same way this fact is expressed by the number of thousands of fibers per square millimeter of the cross-section of the different ventral roots of the cord, which ranges from 5 in the intumescenciae to about 12 in the thoracic region (see Table II).

3. *Relation of the Number of Nerve Fibers in the Ventral and Dorsal Roots.* The relation between the number of nerve fibers in the ventral and dorsal roots, as estimated by STILLING and enumerated by the author, is as follows:

	Ventral roots	Dorsal roots	Ratio
STILLING (female)	149,058	262,919	1:1.8
Author (male)	203,700	653,627	1:3.2

A large part of this difference in ratio is no doubt due to the fact that STILLING failed to include about 39.64% of the nerve fibers in the ventral roots, and about 60% of those in the dorsal roots, or in other words STILLING's numbers as given above are only about 61% of the ventral and 40% of the dorsal fibers, which were probably present. Another factor is the relatively large size of the ventral roots in STILLING's case, as already mentioned.

In order better to compare the number of fibers in the different ventral and dorsal roots, the curves of Fig. 5 have been constructed from data recorded in Table VI. The ordinates have been obtained by taking the largest number of each series

as 100% and expressing the other areas as percentages of this standard. Each percent in the values thus obtained, is represented by 1 mm. on the axis of the ordinates.

In the curves in Fig 5 one sees the relative number of fibers in each of the dorsal and ventral roots, and it is at once evident that this number undergoes a much greater variation in the dorsal than in the ventral roots.

TABLE VI.

Showing the Number of Nerve Fibers in the Ventral and Dorsal Roots, and Relation Between Them.

	No. of spinal segments	No. of nerve fibers in ventral roots	No. of nerve fibers in dorsal roots	Ratio
Cervical	I	3,406	1,808	1:0.5
	II	4,259	28,375	1:6.6
	III	3,850	27,119	1:7.0
	IV	5,955	27,102	1:4.5
	V	13,548	28,204	1:2.1
	VI	11,794	46,549	1:3.9
	VII	8,913	50,278	1:5.6
	VIII	8,435	50,173	1:5.9
Thoracic	I	7,276	17,891	1:2.4
	II	5,625	14,432	1:2.4
	III	7,235	11,701	1:1.6
	IV	7,625	11,375	1:1.5
	V	6,736	8,352	1:1.2
	VI	6,298	7,155	1:1.1
	VII	5,655	12,325	1:2.2
	VIII	6,074	8,983	1:1.4
	IX	5,789	8,163	1:1.4
	X	7,171	10,612	1:1.4
	XI	7,761	11,403	1:1.5
	XII	7,596	14,125	1:1.9
Lumbar	I	7,944	18,861	1:2.4
	II	6,014	23,640	1:3.9
	III	11,138	31,328	1:2.8
	IV	7,349	39,653	1:5.4
	V	10,366	43,128	1:4.1
Sacral	I	8,598	47,461	1:5.5
	II	4,406	25,545	1:5.8
	III	2,340	17,322	1:7.4
	IV	2,323	8,580	1:3.7
	V	1,702	2,223	1:1.3
Coc.	I	519	761	1:1.4
		203,700	653,627	1:3.2

In Table VI attention is called to the following points :

1. The total number of nerve fibers in the ventral roots of the left spinal nerves is 203,700.
2. The total number of nerve fibers in the dorsal roots of the left spinal nerves is 653,627.
3. The ratio of the number of nerve fibers in the ventral and dorsal roots is 1:3.2.
4. The number of fibers in the dorsal root C. IV and the ventral root C. III is small.
5. The ratio between the number of nerve fibers in the ventral and dorsal thoracic roots (I-XII) is, on the average, about 1:2.
6. The number of nerve fibers in the largest ventral cervical roots (C. V, VI) is twice the average number of nerve fibers in the ventral thoracic roots.
7. The number of nerve fibers in the largest dorsal cervical roots (C. VII, VIII) is nearly five times the average number of nerve fibers in the dorsal thoracic roots. Hence in the nerves supplying the arm, the great gain has been in the number of fibers in the dorsal or sensory roots.
8. The number of nerve fibers in the largest cervical roots, both ventral and dorsal, is greater than that in the largest lumbo sacral roots, ventral and dorsal.
9. The arm, relatively to its weight of muscle, is better supplied with motor nerve fibers than is the leg.
10. The arm, relatively to its dermal area, is better supplied with sensory nerve fibers than is the leg.

In Figure 7 are given curves based on the absolute number of fibers in the ventral and the dorsal roots. They show in a very striking manner the great numerical increase in the sensory fibers innervating the limbs, while the number of motor fibers at the corresponding levels is but slightly increased.

That the difference between the number of fibers in the ventral and dorsal thoracic roots (trunk) is so small, is what might be expected. That the neck should show an increase in the nerve fibers in the dorsal roots, does not require much com-

ment if we bear in mind the relatively high sensibility of the skin of the neck, and the small motor supply to the muscles. But that the roots going to the arm should show a relatively smaller number of sensory fibers than does the leg, needs some

TABLE VII.

Showing the ratio between the number of nerve fibers in the ventral and the dorsal roots of man at different levels in the cord.

	Ventral Roots.	Dorsal Roots	Ratio.
Neck (C. I—IV)	17,470	84,404	1:4.8
Arm (C. V—Th. I)	49,966	193,095	1:3.9
Trunk (Th. II—L. I)	81,509	136,487	1:1.7
Leg (L. II—Coc. I)	54,755	239,641	1:4.4
	203,700	653,627	1:3.2

explanation, as the arm has a greater number of sensory fibers per square unit of surface than the leg. The reason for this smaller ratio for the arm is due to the fact that the arm has a much larger number of motor fibers in proportion to its weight than has the leg, and this fact accounts for the ratio found.

4. *Comparison of the Ratio of the Number of the Ventral and Dorsal Roots of the Frog, the Rat and Man.*—Having now the ratio between the number of fibers in the ventral and the dorsal roots of man, it may be of interest to compare this ratio with similar ratios for some lower animals. We have found the ratio between the number of fibers in the ventral and dorsal roots of man to be 1:3.2. This ratio can also be obtained by taking three typical roots only.

	Ventral	Dorsal	Ratio
C. VI	11,794	46,549	
Th. IV	7,625	11,375	
L. II	6,014	23,640	
	25,433	80,564	1:3.2

This being so, we have some ground for believing that the ratio between these three pairs of roots in other animals may also give very closely the ratio between all the fibers in the ventral and dorsal roots.

HATAI (1903) counted in the white rat the nerve fibers in the ventral and the dorsal roots of three pairs of the left spinal nerves (C. VI, Th. IV and L. II), and obtained the ratio 1:2.3.

BIRGE (1882) counted the number of fibers in all the dorsal and ventral roots of three frogs (*Rana esculenta*) having body-weights of 23, 60 and 63 grams respectively. The ratios individually were :

Frog-Weight	Ratio
23 grms.	1:1.07
60 grms.	1:1.14
63 grms.	1:1.24

Average for all three frogs = 1:1.15, or rounding the number for the decimal = 1:1.2.

STANNIUS (1849) states that in fish, as a rule, the ventral roots are larger than the dorsal. There are, however, a number of exceptions to this relation. In estimating the value of this statement in the present instance, it must be remembered that the ratios already given are between the *numbers* of fibers, and that in a comparison like this, the number of fibers and area of roots do not necessarily vary together. In the case of fish, the number of fibers in the roots has not yet been determined in any instance.

Tabulating these results, we have the following :

	Ventral		Dorsal
Frog	1	:	1.2
White Rat	1	:	2.3
Man	1	:	3.2

In this series increasing rank in the zoological scale is accompanied by a relative increase of the number of fibers in the dorsal roots.

5. *Relation Between the Small and the Large Fibers in the Ventral and Dorsal Roots.*—According to the author's estimate, the ventral roots contain 39.64% of nerve fibers the diameter of which is less than $7.5\ \mu$ and the dorsal roots 60%. The comparison may therefore be made as follows :

Diameter of fibers.	Ventral roots.	Dorsal roots.	Ratio.
7.5 μ and greater	122,953	272,451	1:2.2
Less than 7.5 μ	80,747	381,176	1:4.7

It thus appears that, compared with the ventral roots, the dorsal roots are more than twice as rich in fibers, the diameter of which is $7.5\ \mu$ or more and nearly five times as rich in fibers less than $7.5\ \mu$ in diameter.

VII. *On the Relative Areas of the Cross-sections of the Roots Forming the Brachial and the Lumbo-sacral Plexuses in the Male and the Female.*

To determine whether or not the roots of the brachial and the lumbo-sacral plexuses show any difference in size in the two males, (KÖLLIKER and the author) and the two females (KÖLLIKER and STILLING) the spinal roots of which have been measured, I have added the areas of the cross-sections of the four largest ventral and dorsal roots in the cervical and the lumbar regions respectively, as given by the several authors. These results may be arranged as follows :

(a) Relation of the Area of the Cross-sections of Four Roots of the Brachial Plexuses.

	2 males	2 females
Ventral (C. V—VIII)	16.38 mm. ²	16.02 mm. ²
Dorsal (C. V—VIII)	40.04 mm. ²	21.30 mm. ²
	<hr/> 56.42 mm. ²	<hr/> 47.32 mm. ²

From this it is evident that the roots here compared are better developed in the male, and would indicate that the males have a little better motor and much better sensory innervation for the arm.

(b) Relation of the Area of the Cross-sections of Four Roots of the Lumbo-sacral Plexus.

	2 males	2 females
Ventral (L. IV, V and S. I, II)	14.36 mm. ²	17.46 mm. ²
Dorsal (" " " ")	31.04 mm. ²	33.24 mm. ²
	<hr/> 45.40 mm. ²	<hr/> 50.70 mm. ²

From these results it is evident that the roots here compared are better developed in the female, and would indicate that the females have a better motor and sensory innervation of the hips and legs.

These results may also be arranged so as to bring out the relative development of these roots in the brachial as against the lumbo-sacral roots in males and females.

(c) Relation of the Area of the Cross-sections of Four Roots in the Brachial and in the Lumbo-sacral Plexuses.

	Brachial (C. V—VIII)	Lumbo-sacral (L. IV, V & SI, II)
2 males	56.42 mm. ²	45.40 mm. ²
2 females	47.32 mm. ²	50.70 mm. ²

Hence we can conclude in that in the two males the area of the cross-sections of these four roots of the branchial plexus is better developed than that of the four roots of the lumbo-sacral plexus, while in the two females the reverse relation holds true. Although these results are based on too small a number of cases to establish fully a relation of such importance, they are very suggestive, and may serve as a basis for further investigation.

Summary.

(A) AREAS OF ROOTS.

1. The total area of the cross-sections of the ventral roots of the left spinal nerves of a large man was found to be 26.50 mm.² (Table I).
2. Since the total area of the cross-section of the ventral roots of the left spinal nerves is 26.50 mm.², and that of the dorsal roots 54.93 mm.², the ratio of their areas is 1:2.07 (Table V, p. 212).
3. In the cervical region, the third ventral root and the fourth dorsal are interesting because of the diminution in their areas, as well as in the number and diameter of their fibers (Page 225).
4. In the dorsal roots the area of the cross-sections is predominantly a function of the number of fibers, while in the ventral roots the area of the cross-section of the roots is chiefly a function of the size of the fibers (page 225).
5. The largest ventral roots arise one to two segments cephalad to the largest dorsal roots, and the ventral cervical depression (C. III) is one segment cephalad to the dorsal cervical depression (C. IV) (page 224).
6. In two male cords the sum of the areas of the four

largest dorsal and ventral cervical roots (C. V-VIII) is greater than that of the corresponding roots of two females, and also greater than that of the four largest lumbo-sacral roots (L. IV-V and S. I-II) of the same males (pp. 232-233).

7. In two female cords the sum of the areas of the four largest ventral and dorsal cervical roots (C. V-VIII) is less than that of the corresponding roots of the two male spinal cords, and also less than that of the four largest lumbo-sacral roots (L. IV-V and S. I-II) of the same females. This shows that in the male, the roots contributing to the cervical plexuses, and in the female, the roots contributing to the lumbo-sacral plexuses, are the better developed (pp. 232-233).

(B) NUMBER OF FIBERS.

8. The total number of medullated nerve fibers in the ventral roots of the left spinal nerves of the same man is 203,700; and the total number on both sides would therefore be about 407,400 (Table II).
9. Since, according to the author's enumeration, there are 203,700 medullated nerve fibers in the ventral roots of the left spinal nerves, and 653,627 in the dorsal, the ratio of the number of fibers is 1:3.2 (Table VI).
10. In the increase of the nerve supply to the limbs, the gain has been far more in the sensory than in the motor fibers (page 230).
11. The ratio between the number of fibers in the ventral and dorsal roots of man is 1:3.2 (INGBERT), of the white rat 1:2.3 (HATAI); and the frog 1:1.2 (BIRGE). From this we may conclude that probably the relative sensory supply increases as we ascend in the zoological series.

(C) SIZE OF FIBERS.

12. According to the author's estimates, there are about 80,747 (39.1%) fine fibers (less than 7.5μ) in the ventral roots, and 381,176 (60%) fine fibers (less than 7.1μ) in the dorsal roots—in other words, the ratio of

fine fibers in the ventral to those in the dorsal roots is 1:4.7 (page 231).

13. There are about 122,953 (60.90%) large fibers (7.5μ or more in diameter) in the ventral roots, and 372,451 (40%), in the dorsal roots—a ratio of 1:2.2 (page 231).
14. In the ventral roots the fibers, the diameter of which is less than 7.5μ , are most abundant in the thoracic regions.

Fibers less than 7.5μ in diameter	{	C. VI = 12%
		Th. VI = 70%
		S. I. = 14%

(D) NUMBER OF FIBERS PER SQ. MM. OF THE CROSS-SECTION.

15. There are on the average 7,687 medullated nerve fibers to every sq. mm. of the cross-sections of the ventral roots of man against 11,900 for the dorsal roots (page 231).
16. In C. VII-VIII the dorsal roots have nearly twice as many (9,800) nerve fibers per sq. mm. of the cross-section as the ventral (5,500), and in S. I. the dorsal root has more than three times as many (13,800) as the ventral (4,300) (page 216).
17. In the thoracic region the number of nerve fibers per sq. mm. of the cross-section of the roots is nearly the same for both ventral and dorsal roots—namely, about 12,000 (page 216).
18. STILLING'S estimate for the fibers per sq. mm. in the ventral and dorsal roots is close to the estimation here made, for fibers the diameter of which is 7.5μ or more. Fibers below 7.5μ STILLING did not recognize and did not include.

No. of fibers 7.5μ or more in diameter, per sq. mm. in the ventral roots:

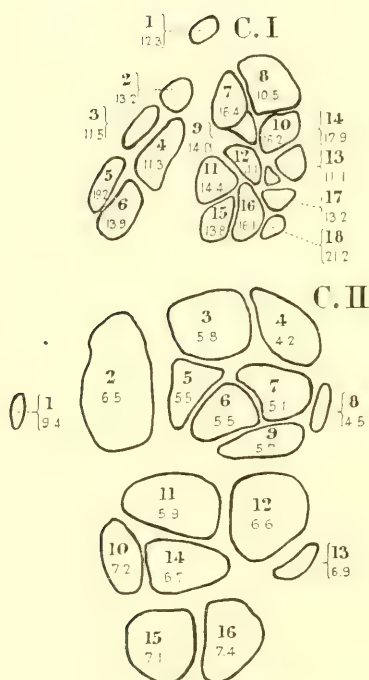
STILLING	4,231
Author	4,556

No. of fibers above 7.5μ or more in diameter, per sq. mm. in the dorsal roots:

STILLING	4,537
Author	4,960

In the following figures (8-38), are given the projections of the ventral roots of the left spinal nerves of man. Their magnification is 33 diameters. Within the outlines of each fascicle are found two numbers: the first designating the number of the fascicle, and the second the number, in thousands, of the nerve fibers per sq. mm. of its cross-section. Thus, in C. I the first fascicle has 12.3 thousands, or 12,300 nerve fibers per sq. mm. of its cross-section. In a few of the outlines of the fascicles is found a letter "c." This is to signify that the fascicle was found to be cut obliquely, and that the number indicating the nerves per sq. mm. is that of some neighboring fascicle similar in constitution, and that the corrected area of this fascicle was obtained by dividing the number of fibers in the fascicle by this number per sq. mm. The outlines are always those of the *uncorrected* projections. In the Tables VIII-XXXVIII accompanying the projections are found the data for each root. These tables have four columns of figures. In the first is found the number given to each fascicle; in the second the area in sq. mm. of the cross-section of each fascicle; in the third the number of nerve fibers counted in the cross-section of each fascicle; and in the fourth the number, in thousands, of nerve fibers per sq. mm. of the cross-section of each fascicle. In cases where a fascicle was found to have been cut obliquely and its area has been corrected, the number indicating the corrected area is placed in the column itself and the number indicating the uncorrected area after it in parenthesis. At the bottom of the table are found the totals. These totals have been brought together in Table II.

TABLES AND FIGURES.



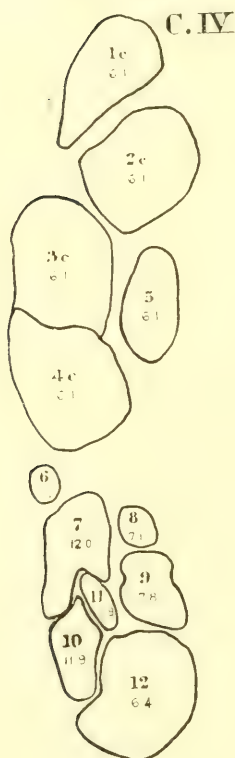
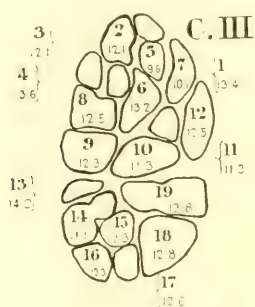
Figs. 8, 9

TABLE VIII C. I.

Number of Fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers in thousands, per sq. mm.
1	.0078	96	12.3
2	.0113	149	13.2
3	.0127	146	11.5
4	.262	296	11.3
5	.0105	202	19.2
6	.0176	245	13.9
7	.0153	251	16.4
8	.0467	493	10.5
9	.0067	94	14.0
10	.0142	231	16.2
11	.0188	271	14.4
12	.0145	161	11.1
13	.0044	49	11.1
14	.0074	133	17.9
15	.0144	199	13.8
16	.0132	213	16.1
17	.0084	111	13.2
18	.0031	66	21.2
Totals 18	.2532	3406	13.4

TABLE IX C. II.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0049	46	9.4
2	.107	659	6.5
3	.0662	385	5.8
4	.0547	227	4.2
5	.0283	158	5.5
6	.0036	187	5.5
7	.0374	192	5.1
8	.0080	38	4.5
9	.0235	134	5.7
10	.0319	232	7.2
11	.0704	415	5.9
12	.0715	478	6.6
13	.0101	73	6.9
14	.0469	318	6.7
15	.0518	369	7.1
16	.0469	348	7.4
Totals 16	.6868	4259	6.2



Figs. 10, 11

TABLE X C. III.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0058	78	13.4
2	.0131	159	12.1
3	.0099	134	12.1
4	.0081	109	13.6
5	.0129	124	9.6
6	.0189	250	13.2
7	.0189	191	10.1
8	.0183	228	12.5
9	.0255	314	12.3
10	.0251	286	11.3
11	.0102	116	11.3
12	.0217	272	12.5
13	.0062	87	14.0
14	.0234	261	11.1
15	.0095	127	13.3
16	.0122	162	13.3
17	.0097	117	12.0
18	.0329	422	12.8
19	.0299	413	13.8
<hr/>			
Totals 19	.3122	3850	12.3

TABLE XI C. IV.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0349 (.0481)	212	6.1
2	.1201 (.1545)	733	6.1
3	.1116 (.1725)	681	6.1
4	.1360 (.1866)	830	6.1
5	.0880	541	6.1
6	.0077	47	6.1
7	.0617	744	12.0
8	.0172	123	7.1
9	.0525	412	7.8
10	.0412	491	11.9
11	.0158	189	11.9
12	.1494	952	6.4
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Totals 12	.8361	5955	7.1

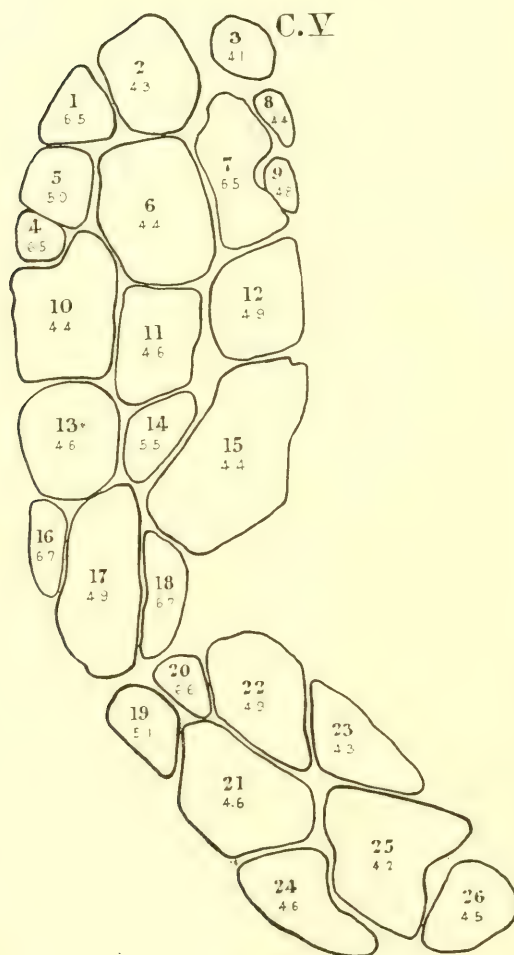


Fig. 12

TABLE XII C. V.

Number of fascicle	Area of fasci- cle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0502	327	6.5
2	.1293	565	4.3
3	.0514	210	4.1
4	.0239	157	6.5
5	.0693	347	5.0
6	.2139	952	4.4
7	.1076	704	6.5
8	.0235	103	4.4
9	.0225	109	4.8
10	.1370	603	4.4
11	.1206	562	4.6
12	.1339	664	4.9
13	.1392	647	4.6
14	.0547	299	5.5
15	.3005	1346	4.4
16	.0351	236	6.7
17	.1774	848	4.9
18	.0509	343	6.7
19	.0621	318	5.1
20	.0309	206	6.6
21	.1923	893	4.6
22	.1462	722	4.9
23	.1121	481	4.3
24	.1328	612	4.6
25	.2065	881	4.2
26	.0909	413	4.5
Totals 26	2.8147	13,548	4.8

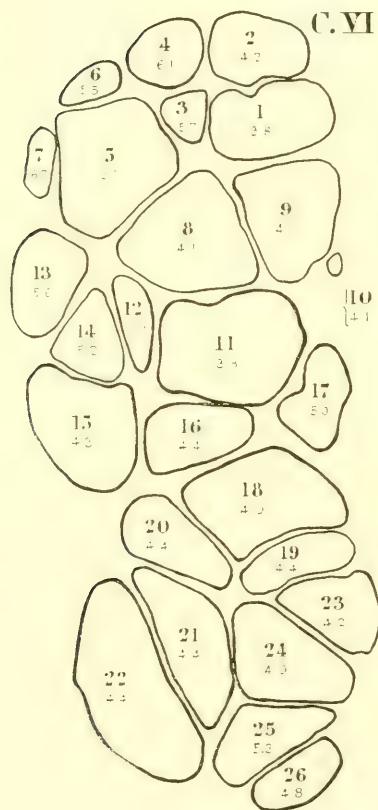


Fig. 13

TABLE XIII C. VI.

Number of fascicle	Area of fasci- cle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.1230	462	3.8
2	.0867	371	4.2
3	.0256	147	5.7
4	.0554	341	6.1
5	.2277	836	3.7
6	.0254	142	5.5
7	.0218	147	6.7
8	.1839	761	4.1
9	.1371	558	4.1
10	.0058	24	4.1
11	.2212	839	3.8
12	.034	202	6.0
13	.0809	454	5.6
14	.0634	329	5.2
15	.1622	728	4.3
16	.0961	426	4.4
17	.0612	306	5.0
18	.1848	744	4.0
19	.0685	302	4.4
20	.0849	418	4.4
21	.1291	576	4.4
22	.2250	990	4.4
23	.0809	341	4.2
24	.1444	578	4.0
25	.0851	451	5.3
26	.0658	321	4.8
Totals 26	2.6893	11,794	4.4

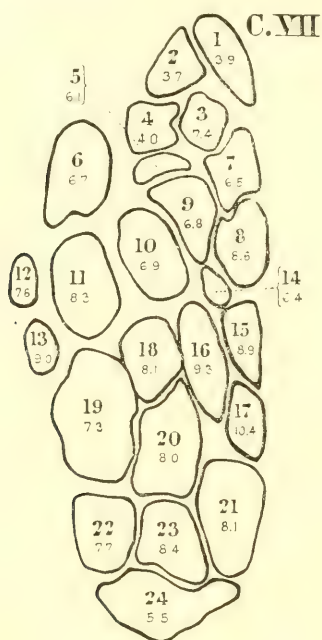


Fig. 14

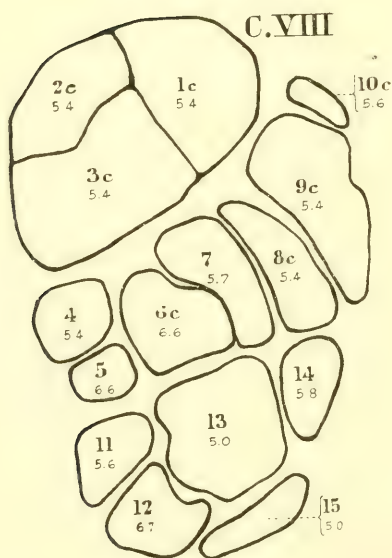


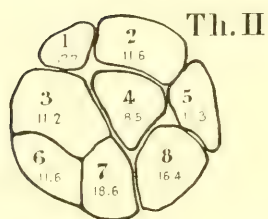
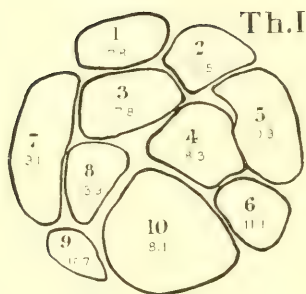
Fig. 15

TABLE XIV C. VII.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0506	202	3.9
2	.0336	124	3.7
3	.0262	196	7.4
4	.0250	101	4.0
5	.0150	92	6.1
6	.0704	475	6.7
7	.0474	312	6.5
8	.0412	398	8.6
9	.0490	332	6.8
10	.0629	439	6.9
11	.0689	575	8.3
12	.0165	126	7.6
13	.0194	175	9.0
14	.0126	81	6.4
15	.0329	291	8.9
16	.0502	469	9.3
17	.0339	353	10.4
18	.0502	419	8.1
19	.1238	912	7.3
20	.0762	612	8.0
21	.0918	749	8.1
22	.0631	489	7.7
23	.0608	501	8.4
24	.0899	500	5.5
Totals 24	1.2165	8913	7.3

TABLE XV C. VIII.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.1650 (.2341)	892	5.4
2	.0842 (.1354)	455	5.4
3	.2111 (.3031)	1086	5.4
4	.0745	407	5.4
5	.0359	241	6.6
6	.1003 (.1276)	662	6.6
7	.1103	628	5.7
8	.0888 (.1162)	506	5.7
9	.1290 (.2032)	697	5.4
10	.0179 (.0273)	97	5.6
11	.0792	449	5.6
12	.0882	595	6.7
13	.2079	1043	5.0
14	.0630	366	5.8
15	.0622	311	5.0
Totals 15	1.5175	8435	5.5



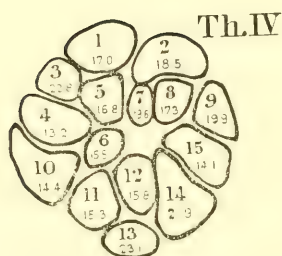
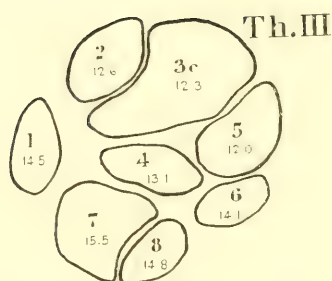
Figs. 16, 17

TABLE XVI TH. I.

Number of fascicle	Area of fasci- cle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0650	508	7.8
2	.0569	596	10.5
3	.0822	641	7.8
4	.0711	908	8.3
5	.0829	591	10.9
6	.0571	638	11.1
7	.0940	1857	9.1
8	.0460	643	13.9
9	.0266	445	16.7
10	.1807	1449	8.1
Totals 10	.7625	7,276	9.5

TABLE XVII TH. II.

Number of fascicle	Area of fasci- cle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0236	418	17.7
2	.0688	803	11.6
3	.0904	1016	11.2
4	.0640	543	8.5
5	.0466	527	11.3
6	.0549	637	11.6
7	.0436	811	18.6
8	.0537	870	16.4
Totals 8	.4456	5,625	12.6



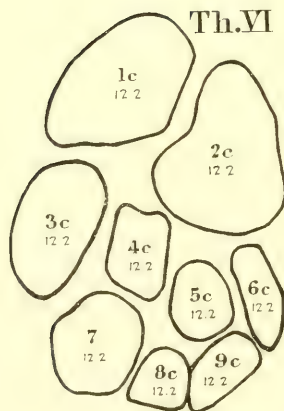
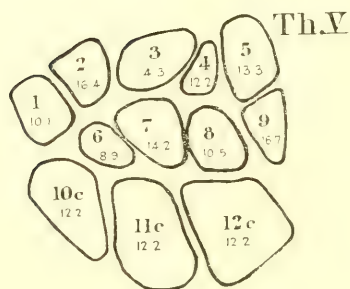
Figs. 18, 19

TABLE XVIII TH. III.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0394	574	14.5
2	.0659	826	12.6
3	.1142 (.1873)	1505	12.3
4	.0566	739	13.1
5	.0789	950	12.0
6	.0398	563	14.1
7	.0945	1473	15.5
8	.0415	605	14.8
Totals 8	.5395	7235	13.5

TABLE XIX TH. IV.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0354	605	17.0
2	.0358	663	18.5
3	.0166	379	22.8
4	.0520	689	13.2
5	.0209	351	16.8
6	.0152	236	15.5
7	.0104	204	19.6
8	.0188	326	17.3
9	.0219	427	19.9
10	.0510	733	14.4
11	.0283	535	15.3
12	.0246	390	15.8
13	.0185	428	23.1
14	.0463	1014	21.9
15	.0458	645	14.1
Totals 15	.4415	7625	17.2



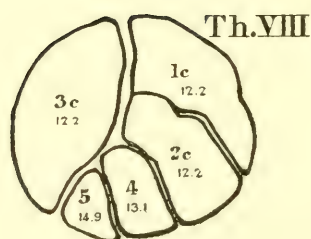
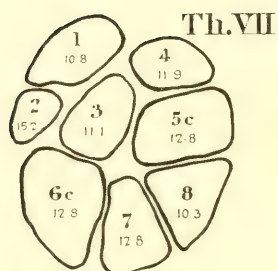
Figs. 20, 21

TABLE XX TH. V.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0361	367	10.1
2	.0309	509	16.4
3	.0510	731	14.3
4	.0119	145	12.2
5	.0462	616	13.3
6	.0216	194	8.9
7	.0490	697	14.2
8	.0434	456	10.5
9	.0288	471	16.7
10	.0466 (.0717)	569	12.2
11	.0809 (.1147)	987	12.2
12	.0815 (.1390)	994	12.2
Totals 12	.5279	6736	12.7

TABLE XXI TH. VI.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0805 (.2175)	982	12.2
2	.0733 (.2428)	896	12.2
3	.1118 (.1393)	1364	12.2
4	.0393 (.0685)	479	12.2
5	.0345 (.0506)	421	12.2
6	.0275 (.0422)	336	12.2
7	.0914	1130	12.2
8	.0286 (.0381)	349	12.2
9	.0279 (.0518)	34	12.2
Totals 9	.5158	6298	12.2



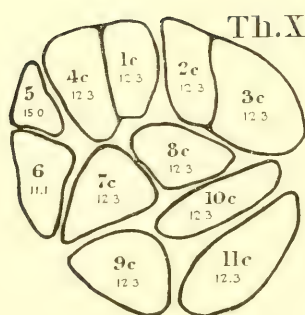
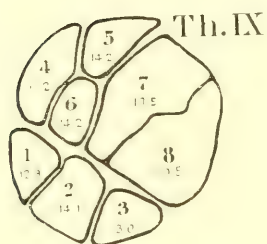
Figs. 22, 23

TABLE XXII TH. VII.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0600	749	10.8
2	.0234	356	15.2
3	.0520	578	11.1
4	.0485	581	11.9
5	.0639 (.0935)	88	12.8
6	.0798 (.1239)	1022	12.8
7	.0582	743	12.8
8	.0784	808	10.3
Totals 8	.4642	5655	12.2

TABLE XXIII TH. VIII.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.1063 (.1540)	1301	12.2
2	.1063 (.137)	1301	12.2
3	.1788 (.2221)	2182	12.2
4	.0630	828	13.1
5	.0309	462	14.9
Totals 5	.4857	6074	12.5



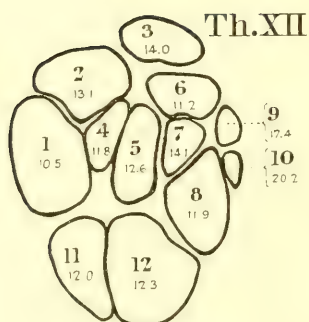
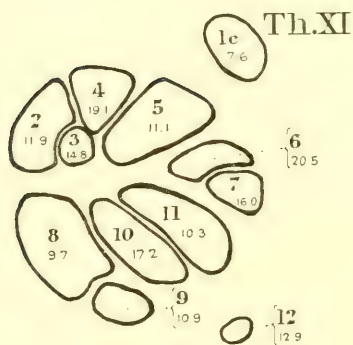
Figs. 24, 25

TABLE XXIV TH. IX.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0382	492	12.9
2	.0474	671	14.1
3	.0355	464	13.0
4	.0535	598	11.2
5	.0383	543	14.2
6	.0275	392	14.2
7	.1148	1205	10.5
8	.1342	1424	10.5
Totals 8	.4894	5789	11.9

TABLE XXV TH. X.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0435 (.0551)	534	12.3
2	.0482 (.0600)	593	12.3
3	.0645 (.1290)	793	12.3
4	.0479 (.0702)	590	12.3
5	.0278	417	15.0
6	.0697	773	11.1
7	.0477 (.0599)	587	12.3
8	.0469 (.0672)	577	12.3
9	.0600 (.0966)	739	12.3
10	.0423 (.0783)	521	12.3
11	.0359 (.1275)	1047	12.3
Totals 11	.5844	7171	12.3



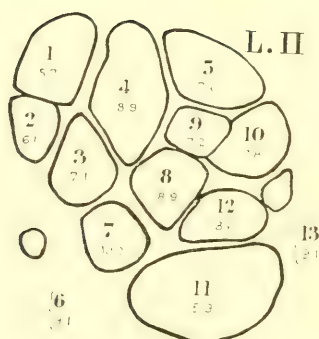
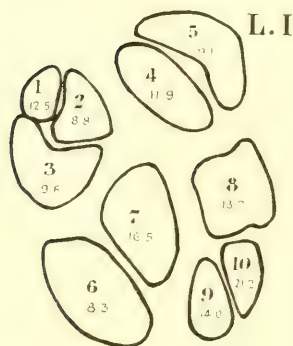
Figs. 26, 27

TABLE XXVI TH. XI.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0236 (.0371)	281	7.6
2	.0586	691	11.9
3	.0150	222	14.8
4	.0356	682	19.1
5	.0813	1216	11.1
6	.0286	587	20.5
7	.0239	474	16.0
8	.0925	904	9.7
9	.0236	258	10.9
10	.0655	1131	17.2
11	.1094	1207	10.3
12	.0084	108	12.9
Totals 12	.5660	7761	13.7

TABLE XXVII TH. XII.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.1026	1077	10.5
2	.0682	898	13.1
3	.0426	598	14.0
4	.0235	278	11.8
5	.0462	586	12.6
6	.0408	461	11.2
7	.0199	281	14.1
8	.0617	737	11.9
9	.0119	207	17.4
10	.0076	154	20.2
11	.0631	761	12.0
12	.1099	1358	12.3
Totals 12	.5980	7596	12.9



Figs. 28, 29

TABLE XXVIII L. I.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0212	264	12.5
2	.0354	314	8.8
3	.0682	659	9.6
4	.0814	971	11.9
5	.0877	834	9.1
6	.1264	1051	8.3
7	.0924	1530	16.5
8	.0862	1181	13.7
9	.0360	507	14.0
10	.0299	633	21.2
Totals 10	.6648	7944	11.9

TABLE XXIX L. II.

Number of fascicles	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.0801	463	5.7
2	.0397	244	6.1
3	.0580	414	7.1
4	.0998	806	8.9
5	.0839	636	7.6
6	.0084	76	9.1
7	.0454	455	10.0
8	.0514	462	8.9
9	.0313	228	7.2
10	.0591	461	7.8
11	.1871	1109	5.9
12	.0549	471	8.6
13	.0108	99	9.1
Totals 13	.8099	6014	7.4

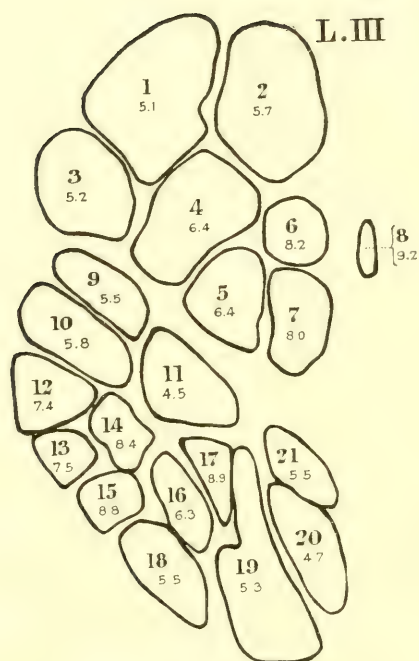
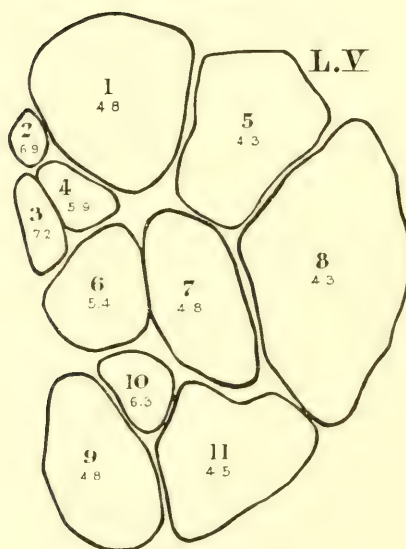
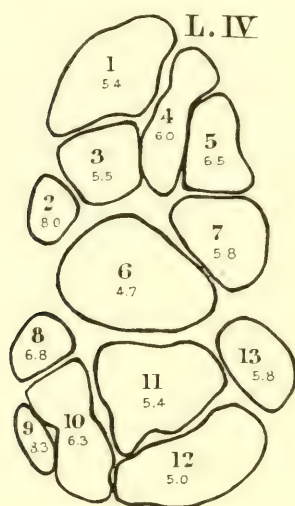


Fig. 30

TABLE XXX L. III.

Number of fascicle	Area of fasci- cle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.2276	1169	5.1
2	.2012	1145	5.7
3	.1258	652	5.2
4	.1597	1015	6.4
5	.0841	540	6.4
6	.0433	357	8.2
7	.0660	531	8.0
8	.0118	110	9.2
9	.0751	414	5.5
10	.0985	575	5.8
11	.1082	482	4.5
12	.0801	594	7.4
13	.0203	222	7.5
14	.0359	304	8.4
15	.0307	272	8.8
16	.0609	386	6.3
17	.0340	303	8.9
18	.0820	454	5.5
19	.1552	823	5.3
20	.0992	468	4.7
21	.0579	322	5.5
Totals 21	1.8665	11138	5.9



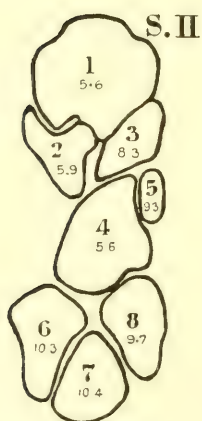
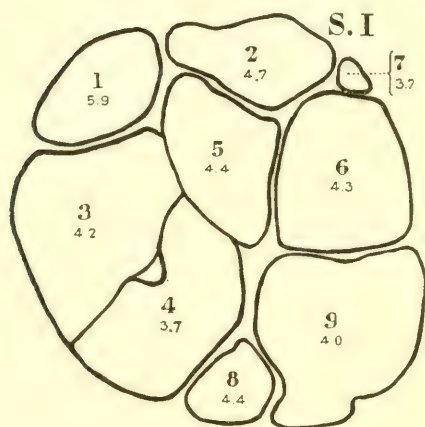
Figs. 31, 32

TABLE XXXI L. IV.

Number of fascicle	Area of fasci- cle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.1455	792	5.4
2	.0312	251	8.0
3	.0851	465	5.5
4	.0862	518	6.0
5	.0654	447	6.5
6	.2064	1144	4.7
7	.0986	571	5.8
8	.0408	279	6.8
9	.0216	179	8.3
10	.1062	666	6.3
11	.1562	854	5.4
12	.1548	784	5.0
13	.0680	399	5.8
<hr/>			
Total 13	1.2660	7349	5.8

TABLE XXXII L. V.

Number of fascicle	Area of fasci- cle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fiber, in thousands, per sq. mm.
1	.3122	1490	4.8
2	.0175	121	6.9
3	.0392	283	7.2
4	.0503	300	5.9
5	.2940	1270	4.3
6	.1436	770	5.4
7	.2165	1039	4.8
8	.5491	2392	4.3
9	.2334	1106	4.8
10	.0529	335	6.3
11	.2569	1260	4.5
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Totals 11	2.1656	10366	4.8



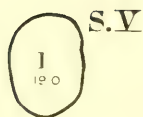
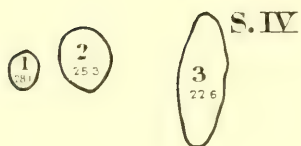
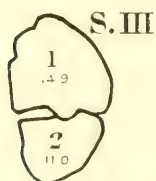
Figs. 33, 34

TABLE XXXIII S. I.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.1568	836	5.9
2	.1607	753	4.7
3	.3596	1626	4.2
4	.2823	1043	3.7
5	.2073	903	4.4
6	.2969	1281	4.3
7	.0081	74	3.7
8	.0975	424	4.4
9	.4106	1658	4.0
Totals 9	1.9798	8598	4.3

TABLE XXXIV S. II.

Number of fascicle	Area of fascicle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
1	.1695	960	5.6
2	.0580	346	5.9
3	.0377	313	8.3
4	.1489	829	5.6
5	.0121	113	9.3
6	.0660	679	10.3
7	.0577	598	10.4
8	.0582	568	9.7
Totals 8	.6081	4406	7.2



Figs. 35, 36, 37, 38

TABLE XXXV S. III.

	Number of fascicle	Area of fasci- cle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
	1	.1105	1647	14.9
	2	.0627	693	11.0
Totals	2	.1732	2340	13.5

TABLE XXXVI S. IV.

	Number of fascicle	Area of fasci- cle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
	1	.0091	256	28.1
	2	.0309	783	25.3
	3	.0568	1284	22.6
Totals	3	.0968	2323	23.9

TABLE XXXVII S. V.

	Number of fascicle	Area of fasci- cle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
	1	.0901	1702	19.0

TABLE XXXVIII COC. I.

	Number of fascicle	Area of fasci- cle in sq. mm.	Number of nerve fibers in each fascicle	Number of nerve fibers, in thousands, per sq. mm.
	1	.0171	519	30.0

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EDITORIAL.

The comparative method is one of the distinguishing characteristics of modern science. Nowhere has it been more fruitful in its application than in the natural sciences, which assume the unity of nature. Comparison here means that in the midst of the detailed analysis to which science subjects natural phenomena there is an accompanying synthesis. Things, to be compared, must be at once different and yet related. The aim of the comparison is to state more comprehensively the relations as well as to define more accurately the differences. But it is in the biological sciences that the comparative method becomes conspicuously serviceable, since here the doctrine of evolution has come in to reinforce the idea of nature as a unity or system. Here unity means continuity, function becomes significant only through genesis, physiology through morphology, and homology gives to comparison a meaning it never could have had so long as it expressed simply superficial resemblance. But a still further step is implied in the comparative method, a step which is best represented in what have been called the hyphen sciences such as astro-physics, physical-chemistry, psycho-physics, physiological-psychology. Without prejudging a movement which is still in its infancy, it may be said that the significance of this tendency is likewise toward an organic interaction between the various sciences, an interaction which promises to be most fruitful and, in the present period of scientific specialization, is greatly needed. It is one aim of this *Journal* to contribute to this development of the comparative method by bringing together researches which, both from the structural and the functional sides, will show what is meant by the evolution of action.

* *
*

Action is a category common to all science, whether we are dealing with the motion or energy of physical science, with the "reactions" so-called of living organisms in the case of tropisms, reflexes, and instincts, or with the "mental processes" or "mental activity" so vaguely conceived at the present time under the figure of a "stream of consciousness." OSTWALD'S recent attempt to subordinate the psychical to the idea of energy is indicative of the demand for a category of action which may serve as a platform upon which the various sciences may get together to discuss those important problems where their respective fields overlap. BALDWIN'S conception of "psychophysical evolution" and of "bionomic" and "psychonomic" forces is a similar attempt to find a basis upon which we can discuss the problems of mutual interest to biology and psychology, without raising metaphysical issues. The evolution of action, then, in the application of the comparative method to neurology and psychology, means the evolution of the organism, especially of the nervous system, as a machine for converting stimulus into response, as a mechanism susceptible to, and in turn mediating, measurable changes in the phenomenal world. Whether mental process is simply a phase of action and, if so, in what sense this is true, are questions which here are not raised, the position taken by this *Journal* being simply that for the comparison of the mental and the neural, the two sets of phenomena must be facts of the same order. The facts of comparative psychology, as truly as the facts of comparative neurology, are acts or reactions, whether or not, in the last analysis, we distinguish the "psychic" as distinct from the "psychological" and "physical" facts, which latter are here brought into comparison.

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The Carnegie Institution has established a Department of Experimental Biology under the charge of Professor C. B. DAVENPORT, now of the University of Chicago. In this Department two Stations have already been arranged for. One at the Dry Tortugas, Florida, under charge of Dr. A. G. MAYER, will undertake the investigation of tropical marine faunas. The

other at Cold Spring Harbor, Long Island, will be devoted to an experimental study of evolution. This Station will be on the grounds lying between the New York State Fish Hatchery and the Biological Laboratory. About twelve acres of ground have been leased for a period of 50 years and through the co-operation of generous neighbors the use of much additional land, both forest and pasture, will be available. A building of brick, about 35 by 60 feet, will be erected on the ground to serve as administrative quarters and for the breeding of some of the smaller animals and plants. An experimental garden of about an acre, completely covered from access of birds by wire netting will be started at once, and there will be two acres of supplementary gardens.

The staff of the Station will consist of Professor DAVENPORT as Director (who will retain for the present also the direction of the Biological Laboratory); Mr. FRANK E. LUTZ, who will have charge chiefly of biometrical variation investigations; Dr. GEORGE H. SHULL, who will work chiefly on plants, and of Miss ANNA M. LUTZ, who besides serving as secretary will make certain cytological investigations. The output of the Station will be increased by others residing there for a greater or less part of the year. Professor R. S. LILLIE will thus be in residence during 1904-05. There will also be a class of Associates which will include biologists who receive special aid for work in Experimental Evolution from the Carnegie Institution or whose work is aided by the Station. The Station and its Associates will coöperate in the work and the results of the investigations of the Associates will, in so far as aided by the Station, be published as results of the Station.

The lines of investigation to be taken up by the Station include not only the evolution of morphological characters but also of physiological ones. Especial attention will be paid to the question of the limit of inheritableness of acquired characters, both static and dynamic. It is hoped that results of importance for Psychology and Neurology will be gained of which the readers of the *Journal* may expect duly to be advised.

COLOR VISION.

The frequent appearance of new theories of color vision is sufficient proof that there is still a feeling of dissatisfaction with the theories chiefly in vogue. The most recent candidate¹ for public favor has been somewhat caustically reviewed by Mrs. LADD-FRANKLIN in the *Psychological Review* (X, 5, Sept., 1903) and, as the monograph is still incomplete, notice is withheld. But the occasion is opportune for calling attention to the very excellent and useful summary of this subject published by Professor MARY WHITON CALKINS in *Arch. f. Anat. u. Phys., Physiol. Abt., Suppl.* 1902, entitled "Theorien über die Empfindung farbiger und farbloser Lichter."

We desire, however, first to call attention to what we deem a fundamental error (often in language only, it may be admitted) which serves to introduce more or less confusion into all of the current discussions.

Considered from the purely psychic point of view, such a thing as composition or "mixing" of sensations is impossible, and this will apply with special force to color sensations. As a matter of fact—of immediate experience—any color, shade or tint is a separate discrete fact of apprehension. From a score of shades of red we may select any one as an objective unit and no one of the twenty will be experienced as a mixture. If it be a fact that there are four primary colors in the spectrum by the mingling of which all secondary colors can be produced, this mixing is not a psychological mixing (though it is a psychological mixing so to describe it) and the fact in no way disproves the statement of the discrete and separate character of every color sensation. Black has just as real an experimental independence as though it had a definite wave length as its external occasion.

That this should be so is readily seen on the basis of the writer's equilibrium theory of consciousness. If every conscious state is but the result of an equilibrium of the cortical activities involved, it makes

¹ EGON RITTER VON OPPOLZER. Grundzüge einer Farbentheorie. *Zeits. f. Psychol. u. Physiol. d. Sinnesorgane*, XXIX, 3, 183-203.

no difference whether one color impression was acting or a dozen were coöperating to impress their mode as the dominant in the equilibrium. The result in either case would be a unitary impression or feeling.

But is it not true that all shades of green, for instance, are recognized as phases of one color? To a certain extent this is true. Different kinds of green are all called green, though when placed side by side they seem to differ greatly. But it is impossible for me to say that one out of the many is a *pure* green and the others are mixtures. It does not appear that there is a composition of simple sensations of which one element (say in this series of greens) remains constant and serves to label all of these nuances "green," while a variable element affords a means of identifying one as emerald green and another as grass green, etc. In fact, it is possible to arrange a series of shades which pass imperceptibly from green into blue, as would not be the case if green and blue were fundamentally different sensations in any other sense than are various sensations of green. Such fusion as there is must be infra-conscious—a nervous process or, at least, a process below the threshold of consciousness.

Professor CALKINS, in criticising the HELMHOLTZ theory of color, says "Yellow looks to us simply yellow and does not in the least appear like a mixture of red and green nor like any other color mixture." We would go farther and add that any color or shade whatever looks like itself and by no means like a mixture of other colors. If various shades of green, e. g., resemble each other more than they do some other primary color this is a subjective fact by itself as is the very fact that certain nervous processes give rise to the mode "green" rather than some other mode of sensation (a fact wholly inexplicable like any "genetic mode"). But, as a matter of experience, some shades classed as green *resemble* some shades classed as blue more than they do the extreme shades of green. The fact of such *resemblance* is not to be explained as the result of mixture but as the result of the power of a certain range of color-stimuli to awaken, concomitantly with their color sensations, accessory activities and to call them into sympathetic vibration in the equilibrium.

The basis of resemblance and difference perception is undoubtedly cortical and is a function of the equilibrium resembling those elements upon which we base judgments of position, etc., even though they are not separately perceived.

Now if we attempt a discussion of the nature of the analysis of light into what are called primary colors we are at once struck by the fact that light itself affords us no such analysis. A light wave is not a

composite of three or four wave lengths any more than water is a mixture of two discrete energy-complexes known as oxygen and hydrogen, each with its peculiar properties different from those of water.

It is true that white light can be broken up by a prism into an indefinite series of wave-lengths of which those between certain rates produce a sensation "red" and those lying between certain other limits produce sensations of yellow, green, blue, etc., and that between certain of these colors definite lines of demarkation appear while between green and blue, for example, the boundary is vague. But it is incorrect to say that light is broken up into four primary ingredients by the spectrum. The true spectrum, physically speaking, is a continuous series. Where then is the analysis effected which gives us color?

The answer seems to be plain: It is in the retina. The retina is anatomically a part of the brain wall with the addition of ectodermal structures.

Upon the prevailing theory of the non-specific nature of nerve conduction great difficulties arise as to the subsequent fate of the products of analysis. Indeed it is often claimed that vision offers an exception and that "it is only in the sense for color that occasion arises for making a different assumption, and hence analogy from other cases is entirely without force" (BALDWIN'S Dict. Philos., Vision, p. 3 of reprint). Here, moreover, we must remember that the optic nerve fibers are not homologous with the peripheral nerves but with the associational fibers of the cortex and on the equilibrium (or any other) theory of consciousness the specific quality of the stimulus must ultimately be communicated *via* fibers to the reticulum of equilibrium or other conceived center for unification.

But, admitting that certain segments of the spectrum—i. e. light waves the rates or lengths of which fall between the upper and lower assigned limits—are capable of producing (let us say in the pigments of the retina) a definite chemical reaction, and no other, then the way is open for the application of some one of the numerous chemico-vital theories of the color vision.

Certain possibilities are then to be considered:

- 1) An eye might be so formed that its color-receiving pigment would be chemically affected by any and all rates of vibration between certain extremes and the resultant sensation would be the same in any such event. The chemical product of decomposition or the process of decomposition might be the adequate stimulus to disengage a sensation of light simply. This might be white light or any other

color. The world would seem either light or dark or would be lighter or darker. Such condition is conceivable as actually occurring in case of the pineal eye of some vertebrates or the pigment fleck of lower forms.

1a) Instead of the visual material being competent to react to all rates of vibration, it might be specifically affected by only one kind of light and so in white light and in the colored light corresponding to its reaction capacity there would be sensation, while in all other kinds of light there would be none. This possibility might be considered in some forms of color blindness.

2) The color conditions might be as above but separate stations be developed for producing the local indices or the elements to be used in the formation of space perception. The fusion of several organs of the elementary type resulting in the development of elementary rod cells imbedded in a single pigment would produce this result.

3) We might assume the existence of three or four different pigments or reaction-substances and that each of these is sensitive to only a limited range of vibrations, while all are sensitive to white light in so far as the latter contains potentially their own specific range.

4) It might be assumed that but two kinds of pigment exist, but that during a regeneration phase each of these produces a different color effect from that produced during a degenerative phase, i. e., during the actual decomposition while acted on by light. In this way there would be produced in the nervous apparatus the foundation for four color sensations. This would perhaps require that a third substance should be present for the production of white and black impressions or it might be supposed that simultaneous action of the two substances postulated would be adequate for white production.

5) Still again, it might be supposed that in transition from the simple condition in (2) some of the cellular elements retained the primitive material sensitive to light only, while others had undergone higher differentiation and so were more complex and contained a visual compound of greater molecular complexity capable of several stages of decomposition before losing the bio-photic power. In this case white sensation may be produced either (a) by the effect of homogeneous light acting on those elements (rods) containing the more primitive pigment or (b) as a result of extreme alteration in the complex pigment as an after effect of long or intense stimulation.

Other postulates might be formulated but these may serve to introduce the table which we translate from Dr. CALKINS' paper above referred to.

I. The YOUNG-HELMHOLTZ Theory of Color-Mixture.

Statement.

There are three fundamental colors: red, green, violet.

Colored light is not a simple but a complex sensation, it results from a mixture of colored lights.

Response.

Contrary to psychological color analysis and to observation.

No explanation is given for:

1. peripheral color-blindness.
2. color-blindness in case of feeble illumination.
3. total color-blindness.

II. Theories of Contrast Colors of HERING, MÜLLER and EBBINGHAUS.

There are four fundamental colors: red, green, yellow, blue.

The facts of the color systems, particularly that the two types of red-green blindness are deficiency phenomena, are not taken into consideration.

Mixtures of red and green do not produce colorless light.

There are two pairs of contrasting colors: red-green and yellow-blue.

Colorless light sensations result from the function of a retinal black-white visual pigment (HERING) or through cortical processes (MÜLLER) if two contrast colors have mutually neutralized each other.

See below.

III. Theories that Colorless-Light Sensations are Produced by the Functions of the Rod-Pigment.

There are three color-sensations which are produced by the activities of the cones (V. KRIES) or the decomposition of the visual purple and the retinal pigment (KÖNIG). Colorless light sensations arise in two ways; by irritation of the rods or by combination of more than one color process.

Psychological analysis demands the existence of four different fundamental sensations.

It is not probable that two sensations subjectively completely similar would be produced by two totally diverse retinal processes.

IV. C. L. FRANKLIN'S Theory of Molecular Dissociation.

There are four fundamental color sensations, which are produced by partial decomposition of differentiated molecules of the photo-chemical retinal substance of the cones.

Colorless light sensations are produced by 1) complete decomposition of the undifferentiated rod molecule, 2) of the differentiated cone molecule. The dichromasy of the normal retinal periphery and the majority of cases of partial color-blindness form an intermediate stage in the development.

See below.

To the above Miss CALKINS remarks: It may be assumed from psychological analysis that there are four and not three fundamental colors and that white is not a mixed but a fundamental sensation. This disposes of the YOUNG-HELMHOLTZ theory.

The fact above noted, that a mixture of red and green light does not produce white light is not reconcilable with HERING's theory.

The anatomical structure and distribution of the rods indicates that these structures can produce only colorless light and this confirms the view shared by v. KRIES, KÖNIG and LADD-FRANKLIN.

The fact that rods and cones originally were similar and that the cones differentiated in the course of evolution, makes it probable that a chemical process which goes on in the same way in the rods and cones produces white light and, furthermore, that various phases or stages of this chemical process in the cones are the causes of colored light. These considerations recommend the LADD-FRANKLIN theory of molecular dissociation.

According to the LADD-FRANKLIN theory, the basis for color discrimination is a four-fold chemical process in the cones but white light is simply produced by the decomposition of the elementary form of the pigment, which decomposition may be supposed to produce a stimulus communicable along the fibers of the optic nerve. Certain other rates of vibration are capable of producing a change in the more complicated cone-pigment corresponding to the sensation of "red," "green" "yellow" or "blue" respectively. It may be ventured as a suggestion in line with this theory that, if the complicated pigment of the cones is genetically related to that in the rods, it is also probable that in its process of formation it will pass through a stage like that in the rods. In this event, there will always be material in the cone capable of reacting to white light independently of a decomposition of the proper complicated pigment in its mature state.

Up to this point no psychological question has been raised except in so far as in the use of language there has been an incautious implication that there has been a mixing of sensations. But suppose wave lengths corresponding to red and blue impinge at the same time on the cones, then either the double stimulant causes a new kind or degree of chemical decomposition, or both the red and blue phases of decomposition are going on concurrently in different ingredients—at any rate the chemical resultant of this mixing *is a nerve stimulus different from that for red or blue alone and must be conveyed along the fibers or fibrils of the optic nerve as such*, or else the retinal ganglia, as a portion

of the walls of the brain, may be supposed to convert the complex stimuli into an element of cortical reaction capable of taking a place in the equilibrium directly. There is certainly much in the structure of the retina to suggest coördination of a high order, rather than the view that the sole function is to transmit the stimuli direct to the brain, and it is not improbable that the ganglia serve to impress upon stimuli their specifically *optic* character. The existence of centripetal fibers suggests accommodation processes in the retina itself.

But none of these suggestions removes the mystery as to what actually passes over the optic nerve when we see. If a simple kind of chemical reaction formed by the vibration of *whole* light produces a white sensation, there seems to be no reason to suppose that the other chemical process resulting from the mingling of various fractional light vibrations should go to the brain or receiving center as discrete stimuli each to produce a sensation, which *separate sensations* now unite to form a composite sensation, say of purple. We know no such psychological process as this. Each color sensation is complete and discrete in itself.

C. L. HERRICK.

LITERARY NOTICES.

Mark Anniversary Volume. *New York, Henry Holt and Company*, pp. xiv, 513, 36 plates, 1903.

This volume, which contains in addition to twenty-five papers an excellent photogravure of Professor MARK, bears the inscription, "To Edward Laurens Mark Hersey Professor of Anatomy and Director of the Zoölogical Laboratory at Harvard University in Celebration of Twenty-five Years of Successful Work for the Advancement of Zoölogy from his former Students 1877-1902."

The following papers of the volume are within the scope of this Journal:

Locy, William A. A New Cranial Nerve in Selachians. Art. III, pp. 39-55.

This research is a careful description of a new cranial nerve, homologous with PINKUS' nerve, in *Squalus acanthias*, *Mustelus canis*, *Raja*, *Carcharias littoralis*, *Syphna tiburo* and *Scoliodon terrae novae*. Its existence has also been determined in embryos of *Torpedo* and in other selachians making in all 19 genera and 24 species of adults.

In all the forms described the nerve enters the brain in the median furrow, usually on the ventral surface of the (secondary) forebrain. In *Squalus*, however, it enters midway between the dorsal and ventral surfaces and in the skate on the anterior dorsal surface. The fibers are traced in the brain to a mesial eminence of the infolded pallium.

Peripherally the nerve is distributed to the nasal epithelium, the greater part going to the antero-lateral part of the olfactory cup. The exact termination was not ascertained. In some forms the nerve exhibits a ganglionic enlargement along its course.

Embryologically the nerve has its own independent connection with the epithelium which precedes that of the olfactory nerve.

Locy is inclined to homologize the nerve with the new nerve described by PINKUS in *Protopterus* and by ALLIS in *Amia*—certainly the differences in point of connection with the brain would hardly justify one in seriously doubting the homology. Locy also thinks that "its separateness in origin and differences from all other olfactory radices" would justify its being called a "new nerve" even if it should prove to be an aberrant olfactory bundle. Apropos of this, the fact may be

mentioned that in the adult skate the writer of this criticism has observed a number of medullated nerve fibers in the nerve in question.

It is to be hoped that more information will be gained respecting the precise origin and termination of this nerve, also the precise nature of its ganglionic enlargements.

O. S. S.

Reighard, J. The Natural History of *Amia calva* Linnaeus. Art. IV, pp. 57-109, pl. 7.

The very commendable general standpoint of this work was to study the natural history and especially the behavior of a fish in its natural habitat. Practically all the observations and experiments recorded were made in the field. That this method of working is necessarily a tedious and laborious one and produces results slowly will be apparent to everyone. The present paper stands as a model to show further that the method is capable of producing just as exact and detailed results as any laboratory work can, and of solving problems which never could be solved in the laboratory. The paper is not alone valuable as a considerable contribution to knowledge in a field where very little has been known, but also as an indication of the possibilities in work on the behavior of aquatic organisms in their natural environment.

Amia calva, the form chosen for study, is a fish which spawns in "nests." It was this habit which first aroused the author's interest in the subject, and the bulk of his work on the natural history of the fish has to do with its habits during the breeding season. A very careful, detailed description and analysis of its behavior during this period takes up the larger part of the paper. The nests are shallow circular areas on the bottom cleared of vegetation, and are built by the males, usually at night. Each nest is the property of a single male and is guarded by that male. If a female does not appear the male will finally abandon the nest. The spawning usually occurs at night and is intermittent. The females are not seen on the spawning grounds except when spawning. The behavior during the actual process of spawning is described. After the eggs are laid the male fish guards the nest until the larvae are about 12 mm. long. This stage is reached in about eighteen days, and at about this time the larvae leave the nest. While in the nest the larvae develop peculiar progressive swarm movements. The individual larvae aggregate in a closely packed group, which from a distance looks like a solid black mass. Within this swarm group individuals behave much as do *Paramecia* caught in a drop of weak acid. When an individual comes by chance to the boundary of the swarm it reacts and turns back into the swarm again.

"The larvae, though not progressing continuously as individuals, form a swarm which nevertheless progresses, one way and another, with many internal irregularities. The movement reminds one of the indefinite flowing movements of an *Amoeba*, in which pseudopods are put out this way and that and often withdrawn, but the animal as a whole progresses definitely." This swarm formation and movement is a most interesting phenomenon and presents a number of problems deserving of further study. Particularly interesting would be an experimental analysis of the reflexes and reactions of the individual larvae which result in the composite swarm effect when large numbers of individuals are massed together.

When the swarm of larvae leaves the nest it follows the male, apparently by scent. When separated from the male the schools of larvae do not make progressive movements as a whole, but circle about in the same spot until the male comes back. The larvae at this stage do not respond to a mechanical shock in the water, but at a later stage, when they have taken on bright colors and are from 30 to 40 mm. long, the schools respond very quickly to mechanical shock by scattering and hiding in the plant material at the bottom. The light reaction (negative to strong intensities) is more pronounced in the older, bright colored larvae. As the larvae grow larger the schools are less closely guarded by the males, and finally when they are about 100 mm. in length the schools probably disperse.

The paper is illustrated by a finely executed plate showing the coloration of *Amia* at three different stages in its life history.

R. P.

Eigenmann, C. H. The Eyes of the Blind Vertebrates of North America. V. The History of the Eye of the Blind Fish *Amblyopsis* from its Appearance to its Disintegration in Old Age. Article IX, pp. 167-204, pls. 12-15.

In this, the fifth of his interesting contributions to the subject, Professor EIGENMANN gives a detailed account of the development of the eye of the cave fish *Amblyopsis*. The eggs of this species are of large size and carried in the gill chamber until the embryos are 10 mm. in length. Egg bearing females were taken in March and April. The object of the research was to compare the development of degenerate and of normal eyes, and to determine (1) whether the development of the degenerate organs is direct or palingenetic, (2) whether there is a constant ratio between the extent and degree of phylogenetic and ontogenetic degeneration, (3) the causes leading to these degenerative changes, and (4) whether there is evidence that rudimentary organs are retained by the embryo because they are of use to it, although useless

to the adult. The stages of development of the eye are divided into four periods.

During the first period (from appearance of first protovertebrae to embryos 4.5 mm. long) the optic vesicle and lens are formed as in normal embryos, but there is retardation in cell-division and growth.

In the second period (embryos 5 to 10 mm. long) the optic nerve forms; its diameter is only 12 micra and it does not increase in size. The lens separates from the ectoderm but its cells do not differentiate into lens fibers and degenerate before the end of the period. A rudimentary iris forms from the margins of the optic vesicle; the cavity of the vesicle is practically obliterated, and the choroid fissure becomes a groove which may remain open. In the retina the pigment layers and inner reticular layer are developed; outer and inner nuclear layers are not differentiated, nor are the cones or dividing cells present as would be the case in the normal eye.

The third period (length from 10 to 100 mm.) is characterized by the degeneration of the nerve cells of the retina, the sinking of the eye to a position 5 mm. beneath the surface of the skin, the closure of the pupil and the complete disappearance of the vitreous body. Scleral cartilages show progressive development.

During the fourth period (fish more than 100 mm. long) the scleral cartilages become well developed and the eye muscles show no signs of degeneration. The pigment layer of the retina forms a thin-walled vesicle of considerable size while the nervous layer is less than 0.2 mm. in diameter and is markedly degenerate. In one individual observed the eye was completely disintegrated.

The author concludes "that there is no constant ratio between the extent and degree of ontogenic and phylogenic degeneration." From the rapid degenerative changes observed in ontogeny it is evident that the ultimate fate of the eye of *Amblyopsis* is total distiction.

The incomplete development of the eye is due (1) to retardation and final cessation of cell division; (2) to retardation of morphogenic processes; (3) to the extinction of histogenic activity. All three phenomena weaken as development proceeds. This may be caused by external or internal influences. As, however, the eye remains degenerate in individuals reared in the light, and is well developed in other cave-inhabiting species, the factor of light may be eliminated. There is moreover, no evidence to show that atrophy is due to pressure from other organs or to lack of nutrition. It only remains to conclude that the causes of the degeneration are inherent in the ovum and are inherited by the embryo.

In discussing the law of biogenesis and the significance of rudimentary organs EIGENMANN points out that the eye is not retained by the embryo *Amblyopsis* because it is a functional organ at this stage, since during cave life the eyes are as useless to the young as to the adult.

C. W. P.

Linville, Henry R. The Natural History of Some Tube-forming Annelids (*Amphitrite ornata*, *Diopatra cuprea*). Art. XI, pp. 227-235.

This paper gives a description of the tube-forming activities of the two annelids named in the title. *Amphitrite* constructs a U-shaped tube of mud and sand collected by the tentacles and held in place by mucus. The tube begins as a ring immediately behind the bases of the tentacles and the gills, and as the process of building is continued this ring is pushed backward by muscular action to make room for the materials which are brought by the tentacles. The author calls attention to the curious fact that this annelid is unable to reconstruct a new tube after the whole of its original tube has been removed. This he thinks, is due possibly to the absence of a stimulus from the tube which ordinarily initiates tube-repairing activities. The worm when young possesses an instinct which determines the construction of a tube, but this instinct after the formation of the first tube becomes valueless and disappears, hence when the animal is stripped of its tube it is unable to begin a new one. The presence of even a small portion of the old tube, however, is sufficient to initiate the appropriate tube-building actions.

Diopatra constructs a tube of sand, pebbles, bits of glass or any other material within reach. According to the observations of Dr. LINVILLE, it gives no evidence of selection of materials. The particles gathered are glued together with mucus secreted by the ventral glands. The animal first places a few pebbles in position then rubs the glands over them until they are firmly cemented. If, during the gluing process, the tentacles be touched with a piece of stone the process at once ceases, and the animal begins to gather material again. Thus the tactile stimulus determines the activity. The author mentions several interesting observations in connection with food taking and respiration.

R. M. Y.

Neal, H. V. The Development of the Ventral Nerves in Selachii. I, Spinal Ventral Nerves, Art. XV, pp. 291-313.

While this research by no means clears up definitely the much discussed question of the histogenesis of the peripheral nerves, it nevertheless is a useful contribution and will serve to deter many from ac.

cepting uncritically the results of such recent researches as those of BALLANCE and STEWART and of BETHE.

The method relied upon chiefly was fixation and staining by VOM RATH's fluid, followed by pyroligneous or pyrogallic acid. The research contains a number of careful drawings. It is rather to be regretted, perhaps, that black and white drawings and line reproductions were used. Outlines of cells and fibers are of great importance in such a research and the effect of such a method of illustration must inevitably be to exaggerate their definiteness as compared with the actual preparations.

The first neuroblasts are found to be developed not from rounded "germinative" cells, but from the ordinary epithelial cells of the neural tube. The neuraxone is formed before any migration takes place. NEAL agrees with DOHRN, BETHE and others in asserting a migration of the cells from the neural tube along the ventral root. This view certainly seems to be now best supported and makes it easier to understand the processes of histogenesis and regeneration if such views as those of BALLANCE and STEWART and BETHE be correct. NEAL, however, denies that these migrated cells take part in the formation of the ventral root fibers and believes they form the neurilemma, possibly also contributing to the connective tissue sheaths and the sympathetic. The migration of the cells is shown by the presence of cells half in and half out of the medullary wall, also by their presence in the part of the nerve next the neural tube. NEAL is also inclined to believe that mesenchyme cells contribute extensively toward the formation of the neurilemma.

These migrated cells of the ventral nerve are believed to have nothing to do with the formation of neuraxones because they are peripheral to and with their long axes perpendicular to the fibrous portion of the nerve when the neuraxones are forming most rapidly, because they do not exhibit the staining reactions of the cells of the dorsal ganglia, because they do not undergo the characteristic changes of shape of the latter and because nothing resembling a neuraxone was to be found in their cytoplasm. On the other hand, the spinal ventral nerves in their earliest stages of development certainly *are* processes of medullary cells and devoid of nuclei and the same continuity can be made out later. The number of neuroblasts whose axones can be traced into the nerve also corresponds with the estimated number of neuraxones in the nerve.

These reasons bring NEAL to the conclusion that the process theory of the development of the ventral nerve fibers is the correct one. NEAL thus agrees with the prevailing view of HIS, though differing

from him regarding the earlier differentiation of neuroblasts and regarding the migration of cells into the ventral root from the neural tube. There would seem to be important differences between the histogenesis of the ventral nerves in the shark and the chick when we compare this account with BETHE'S.

O. S. S.

Jennings, H. S. Asymmetry in Certain Lower Organisms, and its Biological Significance. Art. XVI, pp. 315-337.

In addition to the commonly recognized radially symmetrical and bilaterally symmetrical types of organism, there is, as JENNINGS points out, another type of structure which may be called the spiral type, since the organisms necessarily move in a spiral course, or the one-sided unsymmetrical type. An unsymmetrical organism, were it not for rotation about its long axis, would move in a circular instead of a spiral course.

Organisms which move in a spiral course maintain a definite position with reference to the axis of the spiral; the same surface always faces outward, the same inward. In most of the unsymmetrical organisms it is noticeable that reactions do not differ in form according to the location of the stimulus, as in more highly organized animals, but that no matter which side is stimulated the animal always turns in the same direction.

The relation of structure to behavior is considered in detail in case of the Infusoria and Rotifera, and the author concludes that there is always striking adaptation of structure to the "mode of life and movement."

In criticism of the author's conclusions one might say, certainly there can be no doubt of the close correlation of structure with mode of life, but is it so clear that structure is an adaptation to behavior rather than behavior to structure? Rather, it would seem impossible that either could in all cases be an adaptation to the other. Possibly our safest position would be to consider both adaptations to something which is not to be described as either structure or mode of life.

The paper emphasizes the importance of studying structure and behavior side by side, and of attempting to arrive at definite knowledge of their correlation.

R. M. Y.

Floyd, R. A Contribution to the Nervous Cytology of *Periplaneta orientalis*, the common Cockroach. Art. XVII, pp. 341-357, pls. 25-27.

By a careful series of experiments the author has determined the effect of various fixing reagents on the structure of nerve cells from the thoracic ganglia of the cockroach. Tissues fixed in VOM RATH'S

fluid, picro-formalin, VAN GEHUCHTEN's fluid, corrosive sublimate and chrom-oxalic acid showed more or less shrinkage of the cytoplasm and injury to its finer structure. In all the cells of these preparations a central, darkly staining, granular region was demonstrated, and a peripheral zone formed by a network of fibrillae. In the nerve fibers the fibrillae also exhibited anastomoses. Fresh, living ganglia, stained with NISSL's methylene blue and studied in normal salt solution, showed little or no shrinkage of the cytoplasm. They were entirely devoid of a cell membrane, and though the fibrillar networks were clear and distinct, there was no evidence of the darkly staining granules characteristic of fixed tissues. This normal structure was also observed when ganglia were fixed by the vapor of formalin, and when stained with methylene blue and fixed with ammonium molybdate; graded formalin and diffused alcohol are recommended for larger masses of tissue. In agreement with HELD, the author finds that the chromophile granules (NISSL substance) are not normal structures but are formed in the cytoplasm both during post-mortem changes and during the action of most fixing reagents. The substance is not demonstrated by staining after treatment with sodic hydrate nor after prolonged faradization; probably not after strychnine poisoning. Arsenic poisoning causes an increase in the amount of the substance present in the cells.

These observations are at variance with the results of BETHE and VON LENHOSSÉK, who saw the NISSL's plates in living nerve cells of vertebrates. From various other points of evidence BETHE maintains that the NISSL substance is a normal product of the cells. It is unfortunate that the author did not have opportunity to study the fibrillar structures which he describes by more specific staining methods. The evidence of preparations obtained by BETHE's toluidin blue method would not support Dr. FLOYD's statement that a general anastomosis exists between the neuro-fibrillae of nerve fibers.

The conclusions of this paper are of great value. They show that most of the common fixing reagents cannot be depended upon for the preservation of delicate nerve cell structures, and emphasize the necessity, too often overlooked, of studying fresh tissues to control results obtained from fixed material.

C. W. P.

Yerkes, Robert Mearns. Reactions of *Daphnia pulex* to Light and Heat. Art. XVIII, pp. 359-377.

The author defines as phototactic "all those reactions in which the direction of movement is determined by an orientation of the organism which is brought about by the light," and as photopathic, those "in which the movement, although due to the stimulation of light, is not definitely directed through the orientation of the organism." "In both *intensity* of the light, not the *direction* of the rays, is the determining factor.

Daphnias were introduced into a flat dish of water illuminated only by a band of light focussed on the bottom and measuring 1 x 16 cm., one end of which was brighter than the other. The animals swim into an intensity of 100 candle-power and remain there, and they do this even when the adiathermal screen is not used, so that they die of heat within a few seconds after reaching the brightest spot. "There is no evidence of an 'optimal' intensity between 0 and 100 candle-power." The directive influence of light grows no less as the animals progress toward their goal, i. e. there seems to be no "adaptation," nor is there any evidence of fatigue. A sudden change in the intensity of the light is a stronger stimulus than a gradual change. The brighter the light the faster the progress of the animals, and this is due not only to the greater precision of orientation but also (contra DAVENPORT and CANNON) to swifter swimming movements.

Daphnias are negatively thermotactic at a temperature of 28° C. The thermotactic reaction is elicited by the actual temperature of the water about them, whereas the radiant heat accompanying light has no appreciable influence. The thermotactic "movement is not direct, but irregularly wandering. It is, however, in all probability due to differences in the intensity of stimulation for different regions of the animal's body and is therefore in principle the same as the photopathic reaction," or the phototactic.

E. B. H.

Sargent, Porter Edward. The Torus Longitudinalis of the Teleost Brain; its Ontogeny, Morphology, Phylogeny and Function. Art. XX, pp. 399-416.

The interesting longitudinal thickenings of the roof of the mid-brain known as the torus longitudinalis has been the subject of several researches by the above author, whose previous results are here in part summarized and also extended over more forms. A description is given of its variations in certain members of the Siluridae, Cyprinidae, Salmonidae, Amblyopsidae, Gasterosteidae, Atherinidae, Sciaenidae,

Labridae and Pleuronectidae. In general its development is found to vary *pari passu* with the development of the optic lobes and visual apparatus, especially shown by its small size and simple structure in the cave-inhabiting fishes. It is found, in a rudimentary state, in *Amphioxus*, is present also in *Cyclostomes*, is more developed in ganoids, but reaches its climax in teleosts. In the latter the large cells of its homologues in other forms (*Dachkern* and *nucleus magnocellularis*) are replaced by a greater number of smaller cells.

The torus cells "are usually bipolar, but may be unipolar or multipolar. In every case, however, three neurites ultimately arise from the cell, either directly or indirectly by the division of a chief process." The dorsally directed neurites are non-medullated and form two tracts. One of these, the *tractus toro-tectalis*, breaks up in the superficial fiber zone of the tectum, there coming in contact with optic nerve terminals. The other tract, the *tractus toro-cerebellaris*, passes laterad to the dorsal decussation and thence ventrad parallel with the posterior commissure. It is difficult to trace, but SARGENT believes it to be identical with JOHNSTON'S *tractus toro-cerebellaris* in *Acipenser*. "The chief centrifugal neurite, or axone," of the torus cells is somewhat coarser. These neurites form several fasciculi which ultimately "unite to form the fiber of REISSNER which runs posterior into the *canalis centralis* and through the posterior portion of its course gives off branches which enter the ventral part of the cord and probably run to the musculature."

These important relations of the processes of the torus cells are only illustrated diagrammatically by figures. Such schemata should always be supported by drawings of the elements in question as shown in the preparations that we may be sure how far and how precisely the cell processes have been actually traced. It is often surprising upon how few direct observations many an extensive neurological schema rests. Such drawings are especially demanded where the relations are so unusual. This defect in the present instance has been partially supplied by the author's figures in previous articles and will undoubtedly be completely remedied in the more extended publication announced as in press.

The physiological significance, according to SARGENT, of the fiber of REISSNER and of the toro-tectal tracts is that they constitute a short circuit for quick optic reflexes. Such a view rests in part upon the assumption that there are no other "one neurone" paths from tectum to motor nuclei in the cord, which is probably not the case; and that the fiber of REISSNER passes out directly to the muscles. The latter

is asserted above but not demonstrated, though the course of the mesencephalic root of the trigeminus would support such a view. This view hardly furnishes an explanation of the peculiar position of REISSNER'S fiber.

O. S. S.

Parker, G. H. The Phototropism of the Mourning-Cloak Butterfly *Vanessa antiopa* Linn. Art. XXIII, pp. 453-569, pl. 33.

V. antiopa orients itself in sunlight with its head away from the sun and so that a straight stick held vertically at an appropriate point casts a shadow that falls exactly on the length of the butterfly's body. So invariably is the head directed away from the sun that when resting on tree trunks the butterflies face toward the foot of the tree. If the surface on which it rests "is perpendicular to the sun's rays the insect settles without reference to the direction of the rays." Nevertheless, "*V. antiopa* creeps and flies toward a source of light, that is, it is positively phototropic in its locomotor responses." This positive phototropism of flight or other locomotion and negative phototropism in rest are otherwise not unknown.

Now the author finds that the resting animal keeps its wings spread in sunlight and that the position of negative orientation most fully exposes the wings to light and makes the insect conspicuous. The habit is therefore probably a means of bringing males and females together. Furthermore, it is the eyes which govern the reaction, since any part of the body except the head may be shaded without disturbing the animal, which, however, flies away if the head is shaded. This observation is confirmed by various experiments on animals of which the eyes have been painted over. If one eye is blackened, that side of the insect keeps in motion and the body moves "in a circle, with the unaffected eye toward the center." If both eyes are blackened, the insect does not come to rest, but flies upward, showing a negative geotropism which is readily verified on normal individuals in a perfectly dark room.

V. antiopa discriminates little, if at all, between different intensities, much more between lights of different area. It "remains in flight near the ground" and, although in locomotion positively phototropic, does not fly upward toward the sun, "because it reacts positively to large patches of bright sunlight rather than to small ones, even though the latter, as in the case of the sun, may be much more intense." These reactions are probably based on retinal images which the insect gets. If the sun is clouded over the animals fold their wings.

The "heat-rays" of sunlight seem not to influence the reactions, but an actual change of temperature of the air is effective. A marked de-

crease in temperature, as at night-fall, independent of any decrease in light, causes the insets to settle down; and it is probably the daily changes of temperature which make *V. antiopa* retreat into hiding-places at night and emerge in the morning.

It is not true, as has been paradoxically alleged, "that moths, which avoid daylight, fly into a flame at night, while butterflies, which fly by day, do not possess this fatal instinct." Butterflies also fly into a flame. The author does not confirm the hypotheses put forward by LOEB and by DAVENPORT in order to explain this supposed paradox.

E. B. H.

Hyde, Ida H. The Nerve Distribution in the Eye of Pecten Irradians. Art. XXIV, pp. 473-482, pl. 34.

The application of improved methods in histological research to the eye of *Pecten* indicates, according to the findings of Dr. HYDE, that the descriptions of this organ given by PATTEN, HENSEN and others are not entirely reliable.

A brief but clear description of the histology of the organ is given, and the author then turns to a more detailed consideration of the nerve supply and of the retinal elements. The main conclusions of the paper are thus stated: 1. The rods are not, as was formerly supposed, innervated by fibers from at least three series of nerves. "2. The so-called retinophorae are not the visual sensory cells whose peripheral fibers form the basal optic nerve, but they are the supporting cells of the median layer of the retina. 3. The inner ganglionic cells do not connect with the side branch of the optic nerve, but are the nerve-cells of the bipolar nerve elements. 4. The outer ganglionic cells form a single layer whose inner fibers are disposed in a special reticular structure in the retina and whose outer fibers make direct connection with the side branch of the optic nerve."

The author believes that the visual apparatus of the retina is composed of afferent and efferent neurones, and that the rods are true peripheral visual neurones.

The text is accompanied by an excellent plate which gives the general histology of the eye in one figure, and in others the details of structure of the retinal elements, together with their ganglionic connections.

R. M. Y.

THE ASSOCIATIVE PROCESSES OF THE GUINEA PIG. A STUDY OF THE PSYCHICAL DEVEL- OPMENT OF AN ANIMAL WITH A NERVOUS SYSTEM WELL MEDULLATED AT BIRTH.

By JESSIE ALLEN.

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INTRODUCTION.

In the study of animal psychology the attempt is made to understand in their simplest manifestations the psychical factors entering into reactions to stimuli.

With this in view reactions of all grades of intelligence have been investigated. Two different points of view have given opposing interpretations of the phenomena manifested by the lower animals.

M. BINET¹ has observed the reactions of *Paramecia* to acids and alkalis, and has concluded² that an action of adaptation involves spatial perception of the external object, choice between objects and movements of approach or avoidance.

On the other hand, JENNINGS³ gives a physio-chemical explanation of these same reactions. All the movements of approach and retreat are automatically performed without regard to the "pleasure" or "pain" involved. The mechanism of the

¹ BINET. *Psychic Life of Micro-organisms*. Transl., Chicago, Open Court Pub. Co., 1889.

² P. 61.

³ H. S. JENNINGS and E. M. MOORE. *Studies on Reactions to Stimuli in Unicellular Organisms*, VIII. *Amer. Jour. Physiol.*, Vol. VI, 1902.

movements is put into play by the physical or chemical properties of the medium.

The insects exhibit a comparatively complex organization. LUBBOCK and ROMANES attribute a high degree of psychical development to bees, wasps, spiders and ants. Dr. and Mrs. PECKHAM are more conservative, but conclude that there are present memory, spatial perception, and occasional adaptations of means to end.

ALBRECHT BETHE¹ represents the extreme mechanical interpretation of insect activities, believing them to be expressible in terms of immediate sensory stimuli followed by the motor response.

BETHE's principal opponent is AUGUST FOREL,² whose recent work on the ants leads him to conclude "that sensation, perception and association, inference, memory and habit follow in the social insects on the whole the same fundamental laws as in the vertebrates and ourselves. Furthermore, attention is surprisingly developed in insects." These faculties are, however, manifested in a feeble form.

LOEB³ is inclined to attribute a small amount of intelligence to ants. The question here is whether these animals do or do not have any psychical life. The criterion of intelligence now generally used in experimental work with lower animals is that of educability. LOEB⁴ discusses the distribution of the associative processes among the lower animals. When his book was published only tree frogs, among frogs, were known to possess memory.

YERKES,⁵ in an extended series of careful experiments, finds that the green frog has associative processes, but that as-

¹ BETHE. Dürfen wir den Ameisen und Bienen psychische Qualitäten zuschreiben? *Arch. f. d. ges. Physiologie* (PFLÜGER's), LXX, p. 15, 1898.

² FOREL. *Ants and Some Other Insects*. (Translated by W. M. WHEELER.) *Monist*, Vol. XIV, pp. 33-66, 177-193, 1903-1904.

³ LOEB. *Comparative Physiology of the Brain*, 1902, p. 224.

⁴ Loc. cit., pp. 219, f.

⁵ YERKES. *The Instincts, Habits and Reactions of the Frog*. *Harvard Psychological Studies*, Vol. I, 1902.

sociations are very slowly acquired. The sensory elements which enter into them are visual, tactual and kinesthetic. YERKES used a simple labyrinth, testing the frog's memory of a path to water; he kept records of time as well as of movements made. A straight path was learned by a process of selection from random movements of those which led to the desired object.

YERKES' work on the crustaceans stands almost alone. The green crab and the crawfish both profit a little by experience and learn simple labyrinth paths.¹ BETHE had shown that *Carcinus maenas* could not readily learn to inhibit deep-seated instincts.² SPAULDING³ finds that hermit crabs profit by experience with considerable rapidity when visual and taste sensations may be associated.

Upon comparing the fish, the frog and the turtle⁴ YERKES found that the turtle's associations were formed most rapidly, a somewhat complex path being learned in five trials.

Very little other experimental work has been attempted with animals of this grade. TRIPLETT⁵ found that perches can remember a glass partition which has been removed from the aquarium. He verified the possibility of teaching pikes to inhibit their habit of devouring minnows (MOEBIUS' experiment).

DELBOEUF⁶ has observed lizards in captivity and finds that they differ in disposition and intelligence. They can remember people and places, and they seem to possess the higher emotions as fear, love, jealousy.

¹ R. M. YERKES and GURRY E. HUGGINS. Habit Formation in the Crawfish. *Harvard Psychological Studies*, Vol. I, 1902.

YERKES. Habit Formation in the Green Crab, *Carcinus granulatus*. *Biological Bulletin*, Vol. III, 1902.

² BETHE. Das Centralnervensystem von *Carcinus maenas*. II Theil, *Arch. f. mikr. Anat.*, Bd. LI, p. 447.

³ E. G. SPAULDING. Association in Hermit Crabs. *Jour. Comp. Neurol. and Psychol.*, Vol. XIV, p. 49, 1904.

⁴ YERKES. Formation of Habits in the Turtle. *Pop. Sci. Mo.*, LVIII, p. 519, 1901.

⁵ TRIPLETT. The Educability of the Perch. *Amer. Jour. Psychol.*, Vol. XII, p. 354, 1901.

⁶ DELBOEUF. The Affections and Jealousies of Lizards. *Pop. Sci. Mo.*, Vol. L, 1897 and *Revue Scientifique*, Vol. IV, pp. 363-367, 690 and 805.

Animals with complex psychical processes have been studied more extensively than the lowest forms, and the work done here comprises the principal literature in animal psychology. The classical treatises of Principal LLOYD MORGAN are the model and the stimulus for all subsequent investigation. A recent book of his, "Animal Behavior," contains summaries and critical notes of all new literature on animal psychology, and a timely discussion of the current conceptions and hypotheses.

MORGAN, who has worked with chicks especially, finds memory, intelligent adaptations and a considerable discrimination of objects among birds. Besides the numerous researches upon the chick, few other birds have been observed with respect to their psychical processes.

WESLEY MILLS¹ is among the pioneers in the field of experimental psychology. His observations upon a large number of animals, and suggestions concerning the correlation between physical and psychical development, are of especial value as recognizing the problems and methods of most recent investigations.

The employment of the laboratory method of observation and experimentation has led to fruitful results in that, as conditions are known and controllable, explanations of given reactions may be made with a greater degree of assurance.

THORNDIKE has given explicit and clear-cut formulation to the method of experimentation with animals. His free-and-easy psychological terminology, with his desire for a severely scientific interpretation of results, as well as unusual confidence in the meaning of facts observed, stimulate competition, not to say contradiction. My work on the guinea pig has been undertaken from a point of view somewhat similar to that assumed by THORNDIKE; viz., the point of view that the law of parsimony must govern interpretation, and a sufficient number of control experiments must condition every statement made. Reference will be made to specific points of THORNDIKE's work as occasion arises.

¹ MILLS. *The Nature and Development of Animal Intelligence*, 1898.

HOBHOUSE, the latest author in the field of animal psychology, has brought keen psychological analysis to bear upon the results of a close experimental study. A dog, a cat and a monkey furnished the best material, while other animals gave corroborative data which, if not taken by HOBHOUSE himself, were controlled and edited by him.

HOBHOUSE is more generous in his estimation of his animals than is THORNDIKE, perhaps because the psychical manifestations for which he looks are clearly defined and characterized in his own mind. An advanced grade of intelligence is not vaguely suggested by the term "free ideas," but is discussed in concrete and comprehensive statements about "the practical judgment," and the "practical idea." By a practical idea is meant "the function which directs action, not necessarily in accord with habit or instinct, to the production of a certain perceptible result. It is further a necessary part of such an idea that it rests on a perceptual basis, and is capable of being brought into relation with another such idea, for example, as means to end." . . . "The correlation of such an idea with a remoter end, I call a practical judgment."¹

The possession of practical ideas and the ability to make practical judgments HOBHOUSE attributes to dogs, elephants, cats, otter, monkeys and chimpanzees, those being the animals which he examined.

The work of KLINE,² followed by that of SMALL,³ has direct bearing upon the problem of the present investigation. The life habits of the white rat as described by SMALL, present many points of contrast with the habits of the guinea pig. SMALL furnishes a diary of the young white rat, in which its immaturity at birth and subsequent development are described, and later its intellectual development as shown in ability to learn a labyrinth and to solve other simple problems.

In the study of the psychical processes of the guinea pig I have tried to determine:

¹ HOBHOUSE. *Mind in Evolution*, p. 207, 1901.

² *Amer. Jour. Psychol.*, Vol. X, p. 276, 1898.

³ *Amer. Jour. Psychol.*, Vol. XI, p. 80, 1899.

(1) What processes are characteristic of the adult guinea pig.

(2) How these processes develop from birth to maturity.

More specifically, it was undertaken to show what problems could be learned, at what age the most complex problems were first learned (thus affording an indication of psychical maturity), and what elements contributed to the learning of the problem. As far as possible, the purpose was to gain an insight into the psychical processes of the guinea pig.

The problem and method of work were suggested to me by Professor ANGELL and Professor DONALDSON. They have constantly defined the inquiry, and indicated the general bearing of particular observations.

The investigation is a complement to that made by Dr. WATSON in this laboratory, and to his work¹ there will be constant reference; before the close there will be a comparison of our results with deductions from them. I am under obligation to Dr. WATSON for constant suggestions and help, as well as for the method of work.²

However, it is quite essential, both from a psychological and a neurological point of view, that this work should be undertaken. The white rat is born very immature, its eyes are not yet open, it is naked, its nervous system is entirely unmedullated. The guinea pig, a rodent closely related to the white rat is, on the other hand, born very mature. It is quite able to take care of itself at birth, has full possession of all its senses, is well covered with hair, and, as will be seen, its nervous system is almost completely medullated. The psychical immaturity of the white rat is such as would be expected from its physical immaturity; whereas the guinea pig has a comparatively complete mental equipment at birth.

¹ JOHN B. WATSON. *Animal Education, Chicago, 1903.*

² Loc. cit., pp. 5-6.



PART I. THE ASSOCIATIVE PROCESSES OF THE GUINEA PIG.

From the literature we can glean very little concerning guinea pigs in the feral state. Originally from South America, they were brought to Europe for pets soon after the discovery of the new world. They were first named, pictured and described by GESNER in his *Natural History Folio*.¹ GESNER knew it as "indische Kaninchen," or "indische Schweinchen," indicating the current belief that its home was a part of Asia. Many other names were applied to it in the first descriptions. ALFRED BREHM calls it "Huf-pfotler" (hoof- or claw-footed).

The pets brought to England were smooth, short-haired and slender, and are now known as English cavies, or common guinea pigs. When they were interbred with different varieties in the London Zoölogical Garden, and with the French cavy, other breeds were produced, and there are now four varieties recognized by fanciers—the English, Abyssinian, Angora and Peruvian cavies.²

The variety used in this investigation was the English cavy, though individuals of all varieties have been under observation without giving evidence of any characteristic differences in habits or intelligence. In one case a series of experiments was made with a solid red Peruvian (probably not of pure stock, however), and numerous minor experiments were made with other varieties. No difference was found between them and the common guinea pig.

I. Habits of Guinea Pigs.

So far as we have been able to observe, all or nearly all the activities of guinea pigs may be termed instinctive, since they are present from birth and hence are carried out without previous training or experience.³ Certain characteristic modes of

¹ GESNER. *Appendix historiae quadrupedum viviparorum* Conradi Gesneri Tigurini, Zurich, 1554.

² MRS. STANLEY WALKER MIRICK, "All About Cavies," published by *American Stockkeeper*, Boston, 1901.

³ LLOYD MORGAN. *Animal Behavior*, pp. 63-71, 1902.

behavior which develop shortly after birth with the perfection of the muscular coördination, may be termed "deferred characteristics."

Individual differences in habitual behavior of the guinea pig may be considered either as intelligent adaptations, or as accidental variations; probably when these slight modifications are analysed, the more tenable view will be that the majority of the individual characteristics are variations. Individual characteristics show themselves in rapidity of movement, habitual activity, tameness, adaptability to changing situations, and in such habits as climbing, gritting the teeth, squealing, etc.

Certain characteristics become modified and altered as time goes on. One group of guinea pigs at first chuckled a great deal, the cause of which I am unable to state. Apparently the noise was made by the rapid gritting of the teeth. One individual would begin it and immediately every guinea pig in the room would take it up and continue for half a minute or more. Within three months this habit was discontinued almost entirely.

In its diet the guinea pig resembles the rabbit. It is voracious and will gnaw almost anything in the vegetable kingdom. Its foods in the laboratory are carrots, oats, hay, grass, lettuce and parsnips. It gnaws constantly, the wire, the floor, the partition, anything within reach. In this, too, it resembles the rabbit. Its manner of eating and of searching for food would lead one to the conclusion that it is a grazing animal in its natural habitat.

The guinea pig bears constantly, and is quite prolific in confinement. The average number in a litter is two, though litters of one or three occur frequently. The period of gestation is from 65 to 69 days, and the young are weaned about the end of the second week. Growth is retarded by birth for 2 to 5 days. From 5 days to 12 months there is a steady increase in weight. The age of sexual maturity is extremely variable, but seems to be about four months.¹

¹ MINOT. Senescence and Rejuvenation First Paper: On the Weight of Guinea Pigs. *Jour. of Physiol.*, Vol. XII, p. 97, 1891.

A description of the development of the habits in the young, on a subsequent page, will, I think, show that most of the habitual reactions of the guinea pig are of the instinctive type. Fear of specific objects is probably not instinctive; reaction to warning cries seems to be acquired from the mother after birth; and domestication leads to the modification of some sounds, and probably, to a certain extent, to a partial inhibition of running and jumping activities.

The guinea pig is a social animal. When several are put into a cage they huddle together in one corner, and when they are alone in contiguous cages with wire partitions between them, they are generally to be seen as close together as the wire will permit.

As a rule there seemed to be greater activity in the dark than in the light, more freedom of movement being present. Several times I noticed when the light was turned out the animal would immediately begin to eat. This observation is confirmed by a remark of ERNST VON FRIEDL, who, in speaking of the guinea pigs' natural habits, says "They lie down in the long, dry grass where they live, and keep concealed most of the day. They are more night than day animals."¹ The possible differences in activity in the dark as compared with light has been borne in mind during experimentation.

The note of warning is a sharp cry. Usually it is uttered when any dark object passes the window. Once or twice I have known it to be given when a shrill whistle sounded near by. Many visual stimuli will call it forth. At first my reaching my hand to turn on the electric light overhead caused the note of alarm—not of fear. The cry produced instant quiet throughout the room. I have not heard it responded to except by a mother with young who utters a very low "burr-r-r" to them and thus quiets them. The cry of fear is loud and shrill, seeming to indicate nothing of caution or concealment, while the alarm call is softer and more deliberately uttered. Guinea pigs

¹ FRIEDL. Zur Familiens- und Lebens-Geschichte des Meerschweinchens, *Cavia cobaya*, Marcgrave. *Zoologische Garten*, April, 1889.

do not seem to understand the significance of the warning note until they are three or four days old. Now that the guinea pigs are quite thoroughly tamed, both the note of warning and expressions of fear are rarely observed.

Other sounds uttered are series of shrill squeals and cries indicative of hunger. When I enter the room, if it is near feeding time, the little fellows remind me of their presence. When I approach the basket of carrots, and particularly when the sound of cutting reaches their ears, their squeals are urgent and vociferous. Each individual can be recognized by its voice, as there is great individual variation.

If general conversation is ever maintained amongst the guinea pigs at their social gatherings, it consists only in an occasional "ghrr-r-hr," a sort of guttural aspirate sound like a note of perfect content with life. There is a characteristic tone uttered by the male to attract the attention of the female. This is the "coycobaya," which is said to have furnished the South American natives with their name for the animal (Cobaya, Spanish, Cuy or Coy). The female responds with a low, musical "r-rerp-rerp."

If the guinea pig is surprised, or if anything of doubtful character attracts the attention of the whole group, a "burr-r" is uttered, and there is instant quiet throughout the room. If the experimenter keeps perfectly still the guinea pigs remain noiseless for several minutes. If, on the other hand, the customary laboratory occupations go on, confidence is restored and they return to their gnawing or eating.

Observations of the young would lead to the conclusion that fear is not present at birth. No motor expression of fear could be produced by moving objects, or by any noise, or by touching, pushing or striking. The only reactions to sound that seem to be indicative of fear are those produced by a shrill whistle as described later. It must be remembered that laboratory conditions are unfavorable for the awakening of fear in those animals whose only enemies are creatures of the grass and copse.

The hiding instincts of the guinea pigs remind us distinctly

of a time when a quick retreat would bring them under the friendly cover of a tuft of grass or a little hillock. If the experimenter attempts to catch them they dodge under hay or any cover at hand. No cover being forthcoming, the spot next chosen for safety is a corner of the cage where they huddle up and watch proceedings. Unfortunately laboratory cages were not made to harmonize with their particular color effects, so that the desired result of being invisible is not accomplished. In order to study this point a cage was fitted up simulating the scenery of their grassy South American home. To obtain the best conditions the light was rendered dim by a high board fence, while sticks, stones and mounds of earth completed the realism. It is thought, from observations of both young and old under these conditions, that they rely for escape, not so much on protective coloration, as upon hiding under grass in little inequalities of the ground. However, the English variety, which is presumably nearer the original than any other in the laboratory, is particularly harmonious in color with surrounding grassy mounds.

When undisturbed, the guinea pigs wander contentedly around and nibble grass, but let them suspect that an enemy may spring upon them and they approach their food only by making a bold dash out of their retreat, and drag the food back into a dark corner. In the experimental work this was almost invariably the way food was seized from the boxes, even when the environment was uniformly lighted, so that there could have been no immediate advantage in snatching the food backward a few inches. At first my own movements attracted much attention from certain individuals. This has to be taken into account in the first series of experiments, as will be noted. However, when the strangeness has worn off and the work becomes habitual this factor is greatly reduced, if not entirely eliminated.¹

At first perfect quietness in the room is apt to delay reaction with all the individuals upon which I have worked. After

¹ THORNDIKE has discussed the fact that dogs pay more attention to the experimenter and less to the experiment than do cats. *Animal Intelligence*, p. 38.

the food is reached only one or two bites may be taken, and then even if hungry, the guinea pig remains quiet. But if I rattle paper or my keys during that time, or talk to it, it begins to chew and continues to eat.

The movements of the guinea pig are not well adapted to climbing or jumping. As a rule it has a strong dislike to jumping off a board to the floor of the cage. It will look around and try every means of climbing down, and when compelled to jump does so very awkwardly. On the other hand, it will run off the edge of the table if left alone, and fall to the floor. If it happens to have approached the edge very slowly it will not fall; but generally it seems to have not the least idea that the plane surface upon which it runs does not extend over the rest of the universe. In this too, however, there is individual variation. It may be due to the inadequacy of vision. The suggestion has been made by Dr. WATSON that the difference between the rat and the guinea pig in this respect may be due to a difference in the clinging power of the claws, and in the sensitiveness of the feet to touch. At least it may be safely concluded that the guinea pig has no sixth sense¹ which warns it when there is danger of falling.

Observations leads me to believe that vision in the guinea pig serves primarily for orientation, and for detecting the presence of moving objects. I have not been able to formulate experiments to determine this point definitely. All experiments with colored cards, colored light, and distinctively visual stimuli have given ambiguous, not to say negative results.

The monocular vision which the guinea pig necessarily possesses on account of the position of the eyes and the configuration of the nose, undoubtedly prevents the clear differentiation of objects at close range. There is no demonstrable

¹ SMALL discusses the phenomenon as a "sense of support." He says that all young land animals show hesitation when they approach a void (*Amer. Jour. Psychol.*, Vol. XI, p. 80). YERKES finds that there is a difference in the space perceptions of tortoises, land species showing more hesitation when they approach a void than water species. (*Space Perception of Tortoises. Jour. Comp. Neurol. and Psychol.*, Vol. XIV, 1904).



fovea¹ or other modified area of the retina. It seems the most probable hypothesis that vision serves, as said before, for general orientation, and for the organization of a situation in which a stimulating odor forms one of the important elements. That the one reinforces the other, and that both are utilized in ordinary life processes is indicated by the comparison between reactions to a problem in ordinary daylight, and reactions to the same problem in the dark where vision is practically useless. The complete elimination of the food odor, and the employment of only a visual stimulus of food have thus far given negative results.

II. Characteristics of the Developing Guinea Pig.

A. Description of the Young Guinea Pig at Birth.

As stated above, the guinea pig at birth is well covered with hair, its eyes are open, it can hear, smell, touch and taste. Movement is not coördinated, and slight muscular weakness is apparent. Frequently when the little creature stops running one hind leg is left sprawling behind the body. The head is proportionally much larger than that of the adult. There is no fear of an approaching object, such as the hand in front of the eyes, nor of persons. But a shrill squeal like that of a rat causes first an instantaneous jump, and then a twitching of the muscles. This is a momentary reaction; it may be followed by hiding under the mother, but there seems to be no "panic," nor rapidity of movement as if to escape. While this may be an initial stage of fear, still the attitude of the little fellow is quite different from that of the frightened adult.

A carrot or other vegetable food produces no motor reaction toward it, though before the first day is over the small guinea pig will eat grass, bread and milk, and nibble at a carrot.

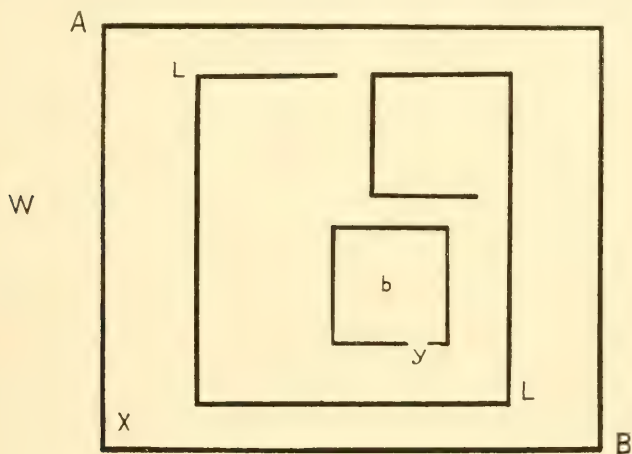
Test I. Is the mother a specific stimulus for her young?

Observation had indicated that carrot or other vegetable food furnished no stimulus toward which the very young guinea

¹ Preparations of the guinea pig's eye were kindly made and examined by Dr. J. R. SLONAKER, in this laboratory, and the above statement is made upon his authority.

pig would react. Therefore I desired to find whether the mother herself could furnish a motive for a solution of a problem. In order to do that the following preliminary experiment was made :

I put guinea pigs two hours old in the experimental cage while the mother was placed in a wire box in plain sight. They could reach her by going to the small opening in the wire. She seemed not to be a stimulus, and there was no attempt to reach her. The little ones' independence of their mother is emphasized by the fact that they ran about quite freely and contentedly for an hour or more away from her. On her part she paid no attention to them, and only in rare cases did any mother gnaw and attempt to reach her young family, even though the little ones had been away from her for an hour or more. In one case I removed a guinea pig five hours old from the mother and left it three hours. At that time the mother was put in an experimental cage within a simple wire labyrinth (Text-fig. 1).



Text-figure 1. Labyrinth I.

A B is the experimental cage used throughout all the experiments. The floor is of wood, and the sides of small wire. It is $3\frac{1}{2}$ ft. long by 3 ft. wide, and usually rests upon two stools or a table at such a level that the light from the windows, *W*, gives uniform illumination over the cage.

The labyrinth, *L L*, is of light weight wire, $\frac{1}{2}$ in. mesh. The wire box, *b*, is 10 by 10 by 10 in., thus being perfectly comfortable for a large guinea pig. It is entered by a small entrance, *y*, just large enough for a little guinea pig.

The little ones were placed at *x*, 24 inches from the opening *y*. The mother was plainly visible through the wire, and could probably have been smelt by a sensitive nose. But she seemed to provide no stimulus leading to definite purposive activity. The young guinea pig gnawed a little at the wire; probably an instinctive reaction, for there seemed to be no recognition of the proximity of the mother, i. e., no association was yet set up between the sight of the mother in this environment and the satisfaction of hunger, if hunger were present. Another female was put in the place of the mother, and the attitude of the young remained unchanged. When the young one was replaced in its home cage, it immediately found its mother and began to suck. The other female was substituted for the mother and the little one attempted to suck her.

At 38 hours the guinea pig squeal in its infantile form is fully developed. Movements are almost as well coördinated as in the adult and there is great activity. The movements about the cage are similar to those of the adult while hunting food. The fore feet creep forward, the bright eyes are on the alert, the belly is flattened to the ground, and the hind part of the body is dragged forward.

The peculiar movement of the guinea pig, so characteristic of the first three weeks of existence, begins to appear on the second day. I can attempt only a description of the movement; what its significance may be, why it arises and disappears as it does, and what form it assumes in the adult I do not know definitely. The guinea pig will run for a few steps, then give a sudden jump forward or in some other direction, then run and jump again. The jump may not be preceded by a running movement; it may be forward close to the ground, or shorter and somewhat more in the air. The jump is so sudden and violent as to be quite startling. It reminds one of the playfulness of a little calf kicking its heels. For some days this is almost the only method of locomotion. It is probably a sign of superfluous activity conspicuous in young animals; and the sudden zig-zags of the course may have facilitated escape at a time when movement could not be inhibited.

At the age of 62 hours evidence of the mother's acting as a specific stimulus is given by the act of the guinea pig in making a real attempt to get to her through the wires of the box. With many individuals such definite recognition of the mother occurs even later.

Development varies greatly in individuals. It seems true without doubt that the larger the guinea pig at birth the more active it is, and the sooner it reaches full coördination and the ability to solve problems presented to it (problems which depend upon activity).

From MINOT's observations¹ it was concluded that the length of gestation is shorter the larger the litter, and the shorter the gestation the smaller the litter. Therefore it is probable that variation in activity and development is a question of maturity, since the small animals are in the large litters. In a litter of two, one pig is apt to be somewhat smaller than the other, and to be a few hours behind it in the appearance of characteristics indicative of progressive stages of maturity, e. g., the jerky running movement which seems to be a good objective criterion of development.

In spite of their social instincts I have never seen the little guinea pigs play together. There is never anything like mock combats among the young such as form a striking feature of rats' play.²

B. Experimental Work.

Introduction.

In the experimental work the kinds of problem to be given the guinea pigs were determined by careful preliminary observation of their natural habits and tendencies. No problem should be given to an animal which involves the inhibition of

¹ Loc. cit., p. 113.

² This small amount of play activity offers a suggestion in favor of the theory of play described in MORGAN's *Animal Behavior*, p. 315. If play is a preparation for the serious defensive and offensive work of adult life, the animal which never makes an attack and has no defence except to run away, could not be expected to spend its youth in sham battles.

a deep-seated instinct.¹ Those experiments in which the time element (the interval between stimulus and response) is of importance should not be foreign to the natural tendencies; all innate proclivities should be seized upon and, so far as possible, should be utilized. The stimuli depended upon with the guinea pig were hunger and desire for company. The former, since it could be carefully controlled and kept a constant factor, was used almost entirely.

It was found that problems whose solution involved activity were solved most readily, while those which involved ingenuity were not solved at all. By ingenuity is meant a very simple process, the putting of two and two together. A paw or a nose may be used to attain an object when other methods have failed. Within narrow limits the guinea pig is very active, many of his movements being made at random. It can select a few movements which have been successful and omit those which have not, so that a path is learned merely by a proper direction of activity. But there is no adaptation of movement to a complication in the problem offered which would involve even a simple new coördination. The absence of all power of adaptation is the absence of all ingenuity.

The guinea pig is a grazing animal, as has been mentioned; it neither digs nor climbs for its food, but runs about. It scarcely ever pulls or pushes obstacles violently, and its gnawing is not adapted to getting into a box. A guinea pig will gnaw for five minutes at a freely swinging door without happening to give it a hard enough push to open it. The gentle swinging of the door back and forth seemed to suggest nothing. All attempts made thus far to give problems similar to those solved by cats and dogs (by THORNDIKE, HOBHOUSE and others) were unsuccessful, in the case of the adult as well as the young.

Even though extremely hungry the little fellow will get discouraged after finding that all the methods he knows fail to reach the food, and he will sit down in a corner of the cage and remain there. At one time I left my brightest guinea pig six

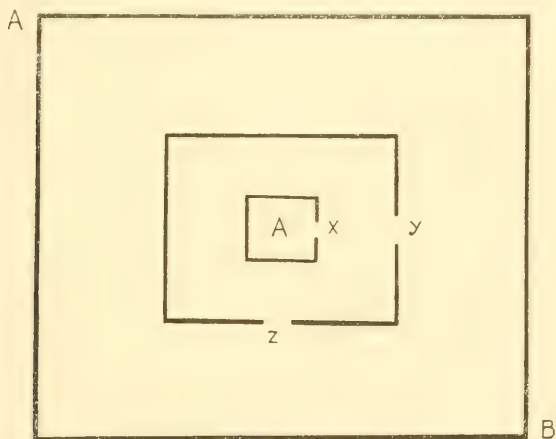
¹ VERKES and HUGGINS. Habit Formation in the Crawfish. *Harvard Psychological Studies*, Vol. I, 1902.

hours on a simple problem of ingenuity,¹ and returned to find it in the same position. Another guinea pig was left all night to solve a problem² but failed.

The problems which could be most successfully solved were simple boxes with doors swinging from the top so that they could be easily pushed open; and various forms of labyrinth. It will be seen that the prerequisite for solution of such problems is activity and not ingenuity. The mentality required was only recollection of the path leading to the food sufficiently distinct to modify successive reactions. The associations which might be formed were controlled as carefully as could be, and will be mentioned under the various experiments.

Test II. Recalling a simple path.

Simple problems of finding the way were given to the



Text-figure 2.

¹ The door of a wire box was to be pulled open by a string running over a pulley and hanging free outside about the level of the guinea pig's nose.

² The problem was to walk up an inclined plane, push open a wooden door hung at the side, pass through a short wooden passage to a wire door also hung at the side, and pushing that open, to walk down another inclined plane to food in the next cage. The food was visible and could be smelt through the wire partition between the two cages.

young guinea pig. The apparatus used was a wire box (6 by 6 in.). The apparatus was placed in the experimental cage (described under Text-fig. 1), so that there was never any crowding or cramped quarters for the animals. In many of the experiments where the path chosen was of importance, and direction of turning and number of random movements were to be observed, the floor of the experimental cage was covered with glazed paper which had been smoked some days before. Preliminary experiments showed that the guinea pig was in no way disturbed by any contact, noise or odor of the paper, and never observed it any more than the usual floor of the cage.

A guinea pig, age 1 day, was placed at *A* within the wire box which had a swinging door, *x*. The larger box had two simple openings at *y* and *z*. The mother was placed outside in the experimental cage. The wires and experimental cage had been carefully freed from all odors by scalding. It will be remembered that at the age of one day spontaneous movement is very slight, and though the smoked paper shows some movement within *A*, the guinea pig did not find its way out. It saw its mother for it usually faced her as she wandered about the cage.

Age, 2 days. Conditions and apparatus the same. Random movements were directed toward finding a way out, and the first solution of the problem was made in 12 minutes.

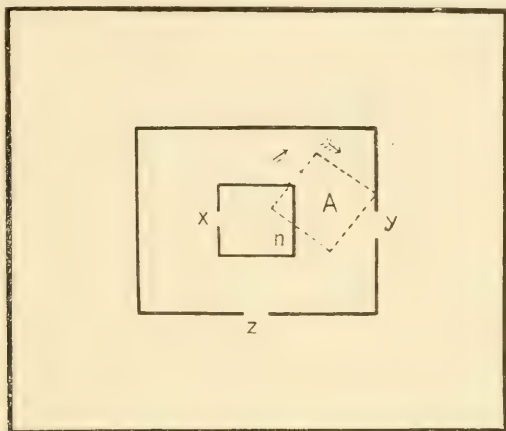
It was replaced. For .25 min. it sat perfectly still with back to the opening and to the mother. Then it turned, and in .083 min. had found her. This is the first proof of the formation of an association.

Upon being replaced for the third time, it found the first opening, but the mother had moved and it went directly toward her. Finding the wire in the way, it went to the second opening, *y*, as usual. Time, .75 min. Few random movements here occurred.

Test III. Alteration in habit.

The experiment was then modified, and the swinging door turned from the opening.

When put inside, the guinea pig immediately pushed the wire at the point where the swinging door had been before, and so pushed the wire box against the other wire (as in the dotted lines, Text-fig. 3), thus cutting off one path to the second opening.



Text-figure 3.

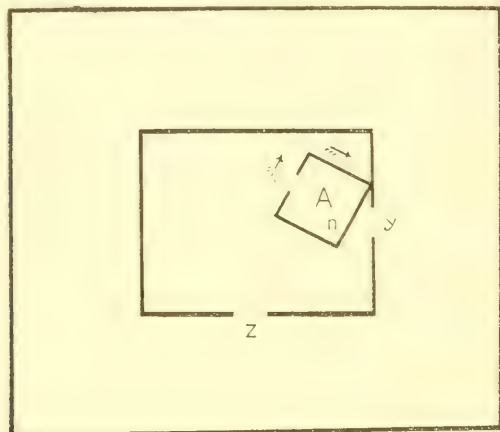
It still scratched and gnawed at the old place, but failing to get out, set out on an exploring tour. In 1.33 min. it had found the door. It then ran around the box in the direction of the arrows to get out at *y*, but found itself shut off there. It began to look again, and in .58 min. had found the opening at *z*. Total time, 2.083 min.

Replaced in A (Text-fig. 4).

The guinea pig sat perfectly still for 1.91 min. Then it turned around and pushed gently at the point where the door had been in the first problem. Not finding the wire to swing easily, it turned directly back and pushed the door open without any random movements. Time, 2.16 min. Then it again went in the direction of the arrows, and found its way closed; then turned and immediately found the opening at *z*. Total time, 2.5 min. The smoked paper showed a minimum of random movements.

Results: At the age of two days there is unquestionable evidence of recollection. It will be noticed that the random movements made in the last trial are almost identical with those

of the other trials, except that minor random movements have been eliminated, and only the principal movements chosen for emphasis. The guinea pig had not succeeded in getting out by



Text-figure 4.

going in the direction of the arrows, yet this same path was chosen the second time, it having been one of the major movements which, as a group, were previously successful.

Test IV. Does the odor of the previous path furnish the stimulus?

Age, 3 days. There is a possibility that the odor of the path just taken might serve as immediate indication of the path to be chosen again. Therefore the reaction would be mechanical, i. e., in terms of immediate stimulus and response, not of recollection.

In order to test this the odor of previous trips was eliminated by thorough scalding of the wire cages and boxes to be used. The wire cages were then set upon glass instead of smoked paper. The apparatus was set up as in Text-fig. 2.

Time for guinea pig to find his way out, .33 min. No random movements. The apparatus was then set up as in Text-fig. 4.

Time, .83 min., the path being the one chosen on the previous day, i. e., including the major random movements.

Upon a second trial of the problem at this time (the wires,

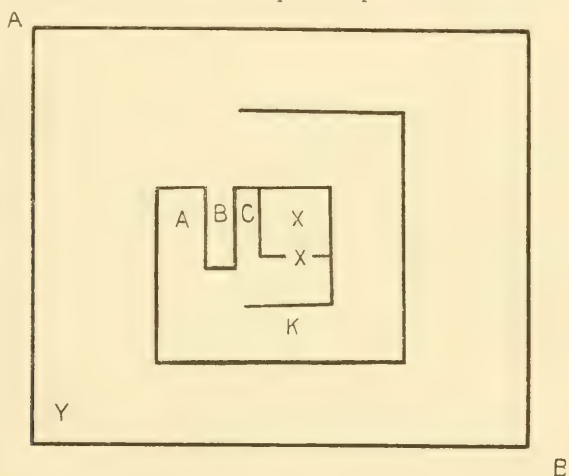
etc., being washed) the time was cut down to .33 min. All random movements were eliminated except a little push at *n*; the route chosen was direct.

One important conclusion, I think, is that the path was not learned by tracking, i. e., that smell did not enter into the formation of the association.

The slow disappearance of random movements suggests that kinesthetic sensations are an important factor in learning a path, though that they are not the only factor is shown by the elimination of unessential movements, indicating that something beside mere sequence of sensations enters into the association.

Test V. Complexity of associations.

The most difficult labyrinth experiment which was to be presented to the adult was now presented to the three days old, in order to determine how complex a path could be learned.



Text-figure 5.

As usual the labyrinth was made entirely of wire. *A*, *B*, *C* are alleys from which there is no exit. The entrance to the wire box, *X*, is very small and is open.

Care was taken to have the whole cage free from any odor. The mother was placed at *X* and the little one at *Y*.

Time for finding the mother in the first trial was 5.166 min.

In the second trial the time was reduced 2 min. There were few random movements, and no blind alleys were entered.

The question arose, How far did the previous experiments with the guinea pig aid it in learning the more complex path?

A guinea pig from the same litter that had never been used for experiment was now tested. It was smaller and not quite so mature as the first one used. When placed in the labyrinth, conditions as for I, it wandered about 45 minutes without finding its way in. This seemed merely chance, as its activity was sufficient to make it wander all over the cage. It paid no attention to the mother, nor had the first one, so far as I could judge, since finding her seemed a matter of accident the first time.¹ I simplified the labyrinth by removing the part directly in front of the entrance (*K*); the mother was found in 33 min., probably by chance.

The apparatus was washed and replaced as in the first instance (Text-fig. 5). Time, 3.166 min.

Repeated. Time, .416 min. All random movements were eliminated. The recollection of the pathway chosen persisted, since experiments on the next day (age, 4 days) with the different individuals showed few random movements and short time reactions.

Close observation of all individuals, as to manner of turning and of moving about, indicates that kinesthetic sensations¹ are a controlling factor in the learning and retention of a path to food. A movement once made and "stamped in" by the pleasure incident to the obtaining of food quickly becomes automatic.

¹ It is hard to know when the young are actually trying to reach the mother (i. e., when she is a specific stimulus). I found definite indication that she furnished a stimulus for the young at the age of 62 hours (p. 309); but even later many of them at times would apparently pay no attention to her, and would not go to her when in the same box.

¹ YERKES has rightly insisted upon the importance of the kinesthetic sensations with animals of a simple psychological organization. (Instincts, Habits and Reactions of the Frog. *Harvard Psychological Studies*, Vol. I).

The experiments were repeated on four different groups of young during an interval of five months. The smaller ones were always a little later in their solution of the problems than their larger brothers, because their movements were neither so rapid nor so numerous. When the way was once found they remembered as accurately as the others.

C. Summary of Work With Young.

1. The guinea pig at birth is physically mature with the exception of slight muscular weakness and inaccurate coordination.

2. That no experimental indications of associative processes were obtained at the age of one day seems to be due to the small amount of activity at that time.

3. All individuals examined learned a simple path to their mother at the age of two days.

4. The most complex problem solved at all was solved at the age of three days, and the recognition of it persisted. There was no indication of increase in complexity of psychical processes after the third day. The problems learned between one and three days depended upon increasing activity, and not upon increasing intelligence.

5. For the reasons previously given, it is probable that kinesthetic sensations are of paramount importance in determining the recollection of a path.

III. *Experiments With the Adult.*

It was found that if the guinea pig had been without food for twenty-four hours, the odor and sight of food were sufficient to induce continuous movement for a considerable length of time, and if mere activity could solve the problem it was most quickly solved under these conditions.

Objections have been made by MILLS¹ and by MORGAN² that experiments upon animals which have been starved beforehand were rendered invalid by the abnormal conditions. In my experimental work on the guinea pig I have not been igno-

¹ *Psychological Review*, Vol. VI, p. 265.

² *Animal Behavior*, p. 151.

rant of these objections, and so far as they are legitimate, they will hold against my work. But I do not think the presence of hunger can be considered as vitiating the experiments. The desire for food is a natural condition, and can scarcely be regarded as an abnormal stimulus in any case. The guinea pig is a phlegmatic animal, insusceptible to considerable variations of temperature and food, as one would naturally suppose from its thick covering of fur, and its ready accumulation of fat upon which it may live. When beginning my experiments even with animals perfectly tame, the problem was to get them to attend to the food in the problem box. The incentive to obtain the food had to be rendered quite strong. My custom was to feed the guinea pigs once a day, about five o'clock in the afternoon; enough hay and oats were left in the cage to last all night and well into the next morning. Those animals with which I intended to experiment were left unfed one day and experimented with at about 2:30 p. m. the next day, when they were fed as usual. This was found to produce the requisite degree of hunger to gain attention to the problem, though there was nothing like the "utter hunger" of THORNDIKE'S cats and dogs. In no case was there "frantic activity" indicative of an abnormal state. Previous observations had demonstrated that hunger any less intense did not succeed in eliminating mere curious exploration, or even quiescence in one corner of the cage.

Upon first introducing the guinea pigs into the laboratory they were wild and easily frightened, and disturbed by my presence, or by any unusual sound or movement. An attempt was made to carry on the experiments in their customary room, but the sight of the other guinea pigs, and when that was shut off, their sound proved a disturbing factor. For that reason the animals to be experimented upon were removed to another room.

A few weeks of persistent and continuous petting, handling and training finally accustomed them to the presence of the experimenter, and gradually the problem came to absorb attention to the neglect of any outside element. Animals born in the laboratory did not have to pass through this preliminary

training. It was found that less disturbance was produced with them by working in the animal room, as all the guinea pigs were now accustomed to the presence of the experimenter, and did not alter their daily routine. Later all experiments were carried on in the animal room without any complications arising.

Test VI. Preliminary.

January 24. I took adult guinea pigs from their cages to another room where conditions of noise, etc., could be governed. Owing to their extreme timidity and fear of handling they did not recover from the removal sufficiently to give any reactions. It then became necessary to tame them, to accustom them to their new surroundings, and to acquaint them with the first apparatus to be used. For this purpose each animal was brought to the experimental room and left in the wire cage several hours daily. Each guinea pig was also handled and petted as much as possible.

January 29. They had become used to the petting and apparatus, and had practically learned the simple problem to be taught them first. They had not solved the problem, but had been taught.

The method of teaching was as follows: When first placed in the cage they remained quiescent in one corner. I placed food very near them, and soon they made a dash for it. Gradually I removed the food farther away, but they were afraid to enter the box. When they became accustomed to my hand I held the food toward them and tolled them to the box. After a few trials they learned to get into the box for the food.

This record of the manner of teaching an animal has interest because of THORNDIKE's observations upon the same subject. He concludes¹ from a questionnaire to animal trainers, that "None of these [the trainers] would naturally start to teach a trick by putting the animal through the motions. . . I see no reason for modifying our dogma that animals cannot learn without the impulse."

¹ *Psychological Review*, Mon. Suppl., Vol. II, p. 72.

In his experimental work THORNDIKE emphasizes the method of learning as that of a selection from a large number of random movements of certain movements which are stamped in by the pleasure of success. I believe, however, that a guinea pig may be taught a trick without waiting for selection from among random movements. What was done was to "control the impulse," and by impulse we mean the amount and direction of muscular innervation.

On the previous Saturday the guinea pigs had remained almost motionless for two hours after being put into the experimental cage. On Thursday the problem had been learned.

A typical series of reactions is given, after the problem has been learned. Until that time the difficulties of fright, strangeness, etc., already mentioned, rendered any time record or other measure wholly meaningless.

The apparatus used was a wire box, 10 by 10 by 10 in., with a wire door hung from the top so as to swing freely in and out. Care was taken that nothing should distinguish the door from the rest of the box. In every case the guinea pig has had no food for 24 hours. The food stimulus used is always carrots freshly cut, which has a strong odor; also it is in plain sight in the wire box. The animal is adult, and in this example is of the solid red Peruvian variety, though mixed with the solid red English.

Jan. 29. ¹	Time.
Door to food box open	.5 min.
Door to food box open	.083 min.
Door to food box open	.066 min.
Door closed	.066 min.
Door closed	.66 min.
Jan. 30.	
Door open	.5 min.
Door open	.25 min.
Door open	.25 min.
Door closed	.25 min.
Door closed	.15 min.
Door closed	.133 min.
Jan. 31.	
Door open	.415 min.
Door closed	.183 min.

¹ It will be observed that throughout the work more than one trial was given during an experiment. At any one time only a little food was given.

The reactions took place almost mechanically. The box seemed to be the thing-to-be-run-into. It was always in the same position. In this way, whether the door was open or closed seemed to make no difference; it was pushed open rapidly when the position of the entrance became an habitual one, and the reaction was not perceptibly lengthened.

From the preliminary test it was concluded that the guinea pig would react to a stimulus under laboratory conditions. The elements entering into the situation were (a) the sight and odor of food; (b) the sight of the box, and association of the general environment with food; (c) the association of a certain series of kinesthetic sensations with the satisfaction of hunger.

Test VII. Distinction of stimuli.

An attempt was made to determine what the stimulus was which induced the reaction to the problem.

The food was covered with a glass dish, and care was taken to eliminate all possible odor from the box. There seemed to be no shyness of the glass dish as it was treated with indifference when left in the cage. Nevertheless, the possibility that fear might not have been observed though present, must be borne in mind.

Jan. 31.	Time.
1.	.5 min.
2.	.75 min.
3.	.083 min.
4.	.083 min.

The first time I did not give any food when the guinea pig got into the box. The effect of this disappointment is seen in the second reaction; at that time I gave food, then removed it quickly. The same was done in the third reaction.

At this point in the experiment it seems certain that a smell stimulus is not necessary to produce the reaction after the situation has been learned.

In order to determine if possible what stimulus is the strongest a choice experiment was introduced.

A dish was arranged in a wire box with the carrot in plain sight but covered with glass. Into another and similar wire

box carrots were placed, lightly covered with sawdust. A third wire box was empty.

Visual	Blank	Olfactory
.25 min.		
.28 min.		1.25 min.

Two wire cages made on the same plan as that first learned but smaller were used. One was empty, the other had a visual stimulus as before. The new boxes were first learned in the ordinary way, by placing the food in one in an open dish. It was first entered in 1.083 min., and the next time in .483 min. The food was then covered with a glass dish and placed in the other cage. The cages were about 1½ ft. apart, and exactly alike. The guinea pig was placed 3 ft. away, facing them. Every time the box with food was entered the guinea pig was given a bite of food, and the food was then transferred to the second cage. During the time of rearranging the apparatus the guinea pig was always removed from the experimental cage.

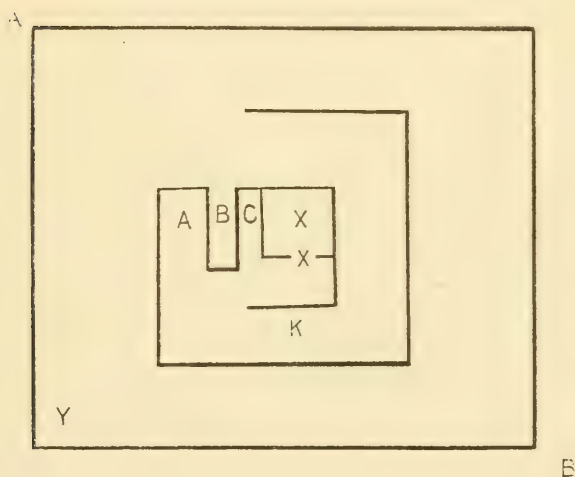
Visual stimulus.	
Box with food.	Box without food.
	.25 min.
	.066 min.
.55 min.	.399 min.
.25 min.	
2 min	
	Feb. 5.
	.166 min.
	.15 min.
	.1 min.
	.33 min.
	.187 min.
	.066 min.
.313 min.	
.313 min.	
.264 min	
	Feb. 6.
.5 min.	.66 min.
.1 min.	.264 min.
.083 min.	.083 min.
	.066 min.

From this experiment we conclude that no choice is present. That is, no immediate discrimination is made between the two boxes. This leads to the inference that the food in itself furnishes no stimulus. But when placed in a given situation the guinea pig reacts to the environment as a whole.

Test VIII. Learning a labyrinth.

The next step in the experiment was to complicate the path to the food, thus to find how quickly a more complex path would be learned.

For this purpose a wire labyrinth was constructed (Text-fig. 6).



Text-figure 6.

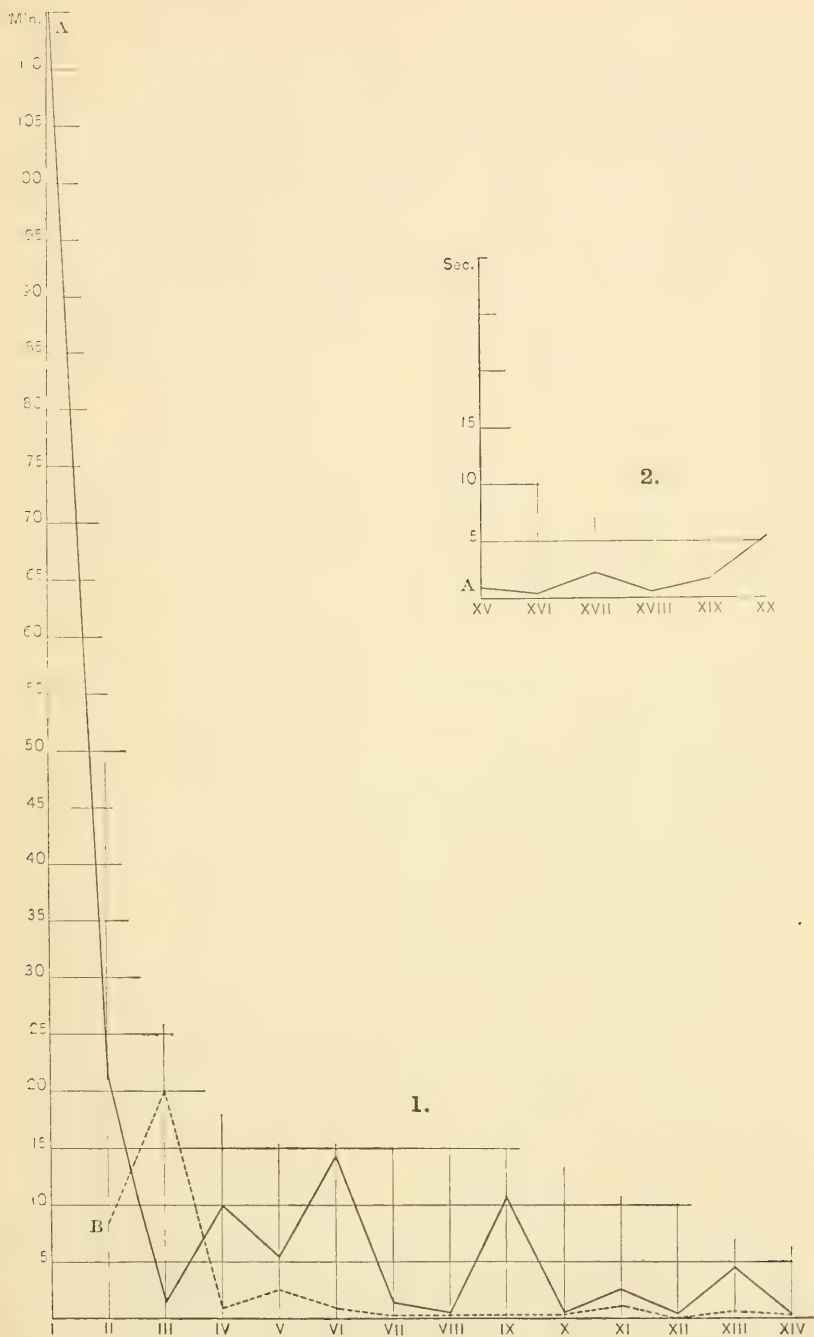
The apparatus is described on page 315. The cage was floored with smoked paper. The guinea pig was placed at *Y*. A typical series of reactions will be given.

Feb. 12. The animal explores the cage, but is perfectly passive most of the time. Found the food in 1 hr. 55 min.

Feb. 13	Time 31 min.
Feb. 14	1.462 min.
Feb. 15	9.75 min.
Feb. 16	5.5 min.
Feb. 20	15 min.
Repeated	1.33 min.
Feb. 25	.5 min.
Repeated	.25 min.
Feb. 26	2.616 min.
Repeated	.83 min.
Repeated	.483 min.
Feb. 27	4.516 min.
Repeated	.55 min.
Feb. 28.	For some reason did not go in. Left 22.5 min.
Mar. 1	.366 min.
Repeated	.2 min.
Mar. 3	2.316 min.
Repeated	.513 min.
Repeated	1.75 min.
Mar. 5	6 min.

In this problem there was choice of two directions to be taken to the entrance. The guinea pig was always put down in a fixed spot, namely at *Y*. It could go to the right or left. As a matter of fact, some individuals learned one way and some the other, and the direction taken was not always the same with the same individual. As a rule, when the problem had been learned the blind alleys were omitted. Attempts to gnaw through the wires at various points were abandoned after the first few times, when another method had proved more successful.

The six guinea pigs which learned this problem, three of which were used at the same time as the example given, were remarkably uniform in their results. There was no sufficiently important variation to deserve remark. The variations which did occur were to be accounted for by difference in tameness, or by some chance noise producing fear and thus requiring time for recovery. Two curves of the time required are here given. (Text-fig. 7.) The time in minutes is indicated on the ordinate, while the divisions of the abscissa represents the numbers of the trials.



1. Curve showing the time of learning the labyrinth, two individuals, A & B
 2. Curve of persistence of the habit, 63 days later.

Text-figure 7.

The paths taken by each individual were preserved by the smoked paper. The most interesting points which the smoked paper shows are two: (1) The number of motions on the part of the adult as compared with the young is much smaller, and are less free. (2) There is a tendency on the part of the adult to keep as close as possible to the wire.

The early movements are different from the adult in kind as well as in number and freedom; the jumping movements mentioned previously are soon lost.

The adult guinea pigs have a peculiar and characteristic method of sneaking across an open space, or of stealing up on food and snatching it back into an imagined retreat. Domestication partially removes this fear of being seen, and the movement does not develop early or strongly in the laboratory young. I think it probable that the "agora-phobia" is an acquired characteristic, or an instinct which, in accordance with JAMES' "law of transitoriness," has lacked fixation by habit, and so has faded away.¹

The typical series of reactions to the labyrinth was completed March 5. On April 20 the same guinea pig was given the same problem, having been free from experiment during the interval. Conditions of hunger were the same as those previously obtaining.

Time required for the solution, 1 min. Some time was lost in exploring the cage, but after once entering the labyrinth only .3 min. elapsed before the food was found. Each turn was made accurately, showing perfect familiarity with the pathway. Two blind passages were barely entered.

April 22, a day having been omitted to preserve the food conditions constant, the times were (1) .33 min. (2) .33 min.

April 24, time, .166 min.

Therefore we conclude from the elimination of random movements and from the short time required, that the recollection of the problem persists at least 48 days, undiminished in its efficiency.

¹ Principles of Psychology, Vol. II, pp. 398-402

On July 27, 63 days later, the same test was repeated with the same animal. Time required, .33 min. Conditions were the same as before. The apparatus was freshly washed, and smoked paper used to show the movements. The only difference was that the guinea pig was taken at the usual feeding time, and it had not been handled for two months.

July 27	Time, .33 min.
July 28	1.33 min.
July 30	.2 min.
July 31	.415 min.
Aug. 3	.166 min.

At this time this and several other of the experiments were repeated on other individuals, and the memory in every case was almost perfect.

Conclusions from the labyrinth experiment.

I. The guinea pig can learn a complex path to food.

II. The time curve for learning is very abrupt for the adult, and for any one individual is also irregular. It tends, however, to reach a minimum at which point it is, after a few trials, nearly constant. In the labyrinth used this minimum will be observed to be .166 min.

III. The curve for elimination of random movements follows very closely the time curve, as random movements necessarily increase the time required.

IV. There are two kinds of random movements: (1) Those made in attempt to reach the food, as biting the wire, running into blind alleys; (2) those of superfluous activity or curiosity, as exploring the cage, running about, and jumping. When the guinea pig seemed in too playful a mood to attend to business, it was a sign that it was not hungry, and therefore conditions were not uniform.

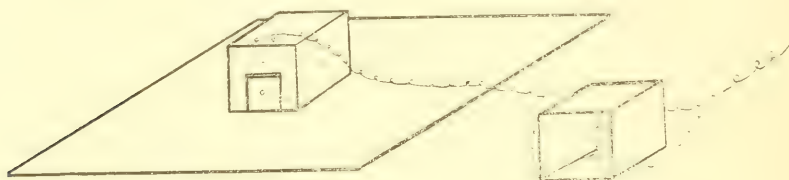
Test IX. Learning without the aid of vision.

Granted that the guinea pig can learn a complex path, the problem arose, What sense elements contribute to this result? What does the guinea pig remember?

The guinea pig may orient itself by means of vision, by

means of smell, or by kinesthetic impressions. It will be remembered that when the simple wire box was placed before the guinea pig, it ran in exactly as it was accustomed to do, although no food was inside. The box itself was then the stimulus, as being associated with food.

To determine how quickly the odor of food alone could set up the association, a series of experiments was designed, in which the visual factor was eliminated.



Text-figure 8.

The apparatus used in this test was a simple wooden box, $6\frac{1}{2}$ by $6\frac{1}{2}$ by $6\frac{1}{2}$ inches, with numerous small holes bored in it (Text-fig. 8). A door was swung by hinges at the top. A copper spring inside the door made contact with a plate in the top of the box when the door was pushed open. Connection was made with an electric light in a dark box entirely outside the experimental cage. The experimental cage was covered with a black cloth frame, and all experiments were performed at night, so that no light should be present. Noises and other accidental disturbances were thus diminished.

In the first series of experiments it was possible, after the reaction had been made and the light turned on, for a faint glow to penetrate the cloth covering of the experimental cage. At a later time these results were verified in the dark room where no light could enter, and the arc connected with the apparatus was so arranged that no illumination of the room was possible.

The typical series given was taken from an adult guinea pig about nine months old, of the smooth English variety. It had not been used before for any experimental work, and therefore the first thing that had to be done was to tame it, and ac-

custom it to being brought upstairs. As usual, the quickest way seemed to be to associate the experience with food. On Feb. 12 it was taken to the dark room at the usual feeding time and put in the experimental cage. After having been left there about half an hour it was returned to the guinea pig room and fed lightly.

Feb. 13. It was taken to the experimental cage, food having previously been placed there. In 5 min. the food was found and was pulled to one side of the cage to be eaten.

Feb. 15. The food was put in a wire box, but was not found. The guinea pig was now becoming tame, and behaved naturally when removed to the experimental room. Fright had disappeared.

Feb. 16. The electric food-box was used with the door open. The food was not visible in the dark, and the door was left open in order that the slight grating of the hinges, the noise of the contact of the spring with the plate, and the touch of the door itself might not frighten the timid animal. The time was recorded from the moment of placing the guinea pig in the experimental cage until the sound of pulling out the food was heard. (When the door to the box was closed the appearance of the electric light gave a more accurate time limit.)

The food was found, seemingly accidentally, in 2.264 min.

Feb. 17. Animal very active. Food not found.

Feb. 18. Door to electric box open. Time .05 min.

Door to electric box open. Time .25 min

Door to electric box open. Time 1.083 min.

Door to electric box open, Time 5.581 min.¹

Feb. 22. Door open. Time 1.85 min.

Feb. 24. Door open. Time 11.88 min.

Repeated. Time .1 min.

Door closed. Time .43 min.

Door closed. Time .35 min.

Feb. 25. Door closed. Time 2.913 min.

Door closed. Time .528 min.

Door closed. Time .43 min.

Feb. 26. Door closed. Time 4.726 min.

Door closed. Time .783 min.

Feb. 27. Rattling of windows in the wind frightened the guinea pig, and therefore no reactions.

Feb. 28. Door closed. Time .83 min.

Mar. 1. Door closed. Time .89 min.

Mar. 2. Door closed. Time .25 min.

Mar. 3. Door closed. Time 1.363 min.

Door closed. Time 1.783 min.

Door closed. Time 1.783 min.

Mar. 5. Door closed. Time .183 min.

Door closed. Time 2.33 min.

¹ This increase in time was probably due to two things; (a) not so hungry

The results of this series of experiments when compared with a similar series taken in the light are these: (1) The range of variation in reaction-time is greater in the dark than in the light; (2) A longer time is required to form a definite habit of entering the cage for food; (3) The average time required, even omitting the excessively long periods, is longer than that required for the analogous experiment in the light. This is true in spite of the greater activity of the animal in the dark and the greater freedom with which exploration is made; (4) It follows, therefore, that the number of random movements is much greater in the dark than in the light. This the smoked paper shows to be almost invariably the case.

Conclusions from the four tests.

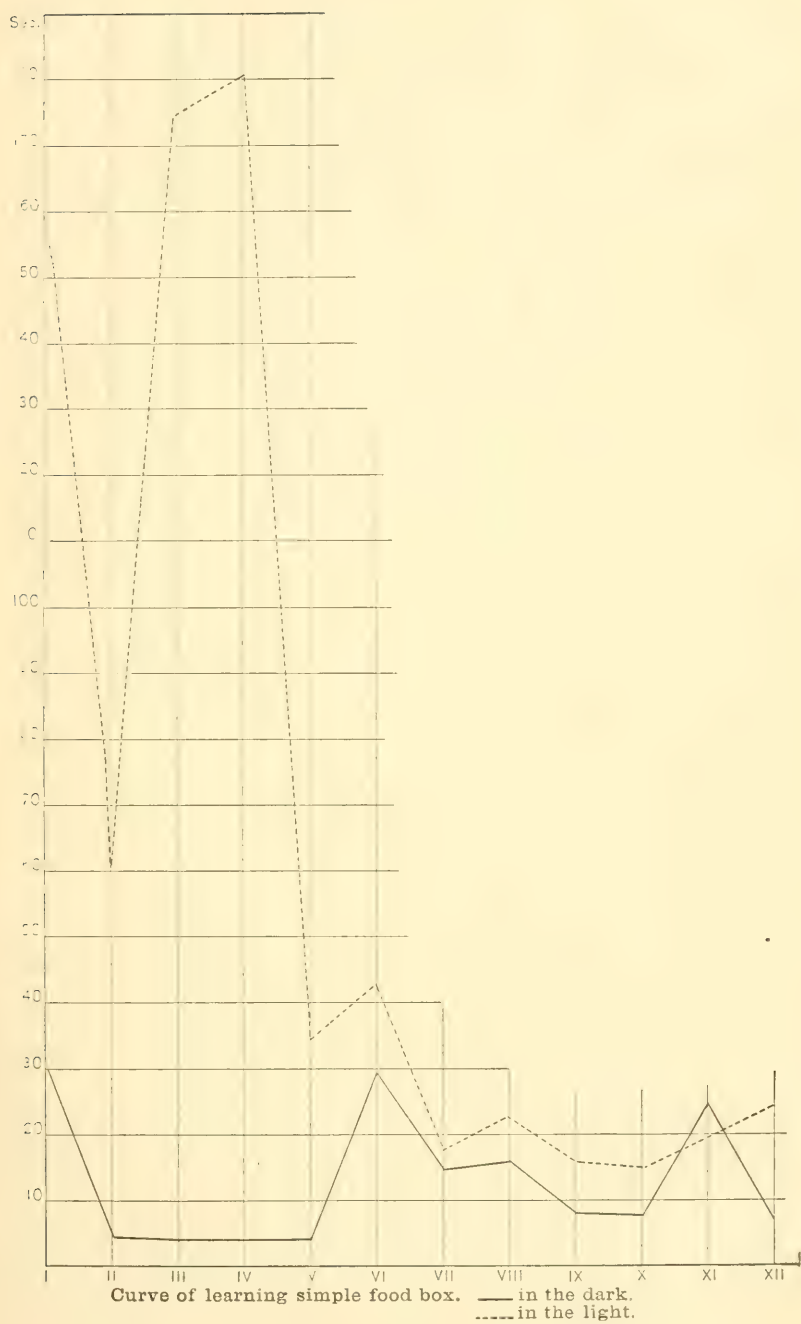
In those tests in which only a visual stimulus of food was permitted in a situation not previously associated with food, there was no attempt to obtain the food; it apparently did not attract attention. Other experiments, particularly the choice experiment of test VII, gave negative results as to the efficiency of a visual stimulus when not reinforced by other stimuli.

From the sixth and seventh tests it was concluded that, after a situation is once connected with food, it is reacted to as a whole with the appropriate movements. An odor stimulus of food is then not a part of the situation essential to the reaction.

From the eighth test we found that the situation might be considerably complicated without diminishing the appropriateness of the reaction. A situation which presents difficulties of the kind which the animal would meet in its natural environment, is rapidly learned and reacted to almost automatically.

The ninth test has shown that vision is an important element in learning the problem, but cannot be the only element, since the problem was learned without it, though more slowly.

after eating the bite or two allowed at each entrance, (b) a little fright and discouragement from being repeatedly removed from food. The lengthened time of reaction was often noticed if the experiments were repeated several times in succession, and therefore too frequent repetition was hereafter avoided.



Text-figure 9.

The paths taken throughout all the experiments by the guinea pigs, their customary accuracy in turning corners, and the general precision of their movements after the problem is learned give unmistakable evidence of the great importance of kinesthetic sensations in the recollection of the path.

Test X. Preference for the dark.

A series of experiments was now tried which did not lead to anything definite, and hence will be only mentioned.

Observation had not indicated any preference of the guinea pigs for the dark side of the cages, or for remaining under cover except when frightened, but the fact that always in the evening they are most active suggested that there might be a preference for dark passages.

A large galvanized iron box was divided into a light and a dark compartment, and an opening was so arranged that the partition in the box divided it also into halves. Food was placed in equal amounts at the distant ends of both compartments, and the guinea pigs were placed outside in the experimental cage. That tracking or any odor other than the food might not complicate the situation, the box and cage were always carefully washed after each trial.

The first few records with two of the four animals tried indicated a slight preference for the dark side; but all the rest of the trials, forty or more, showed the choices of the light side to be equal to those of the dark side.¹

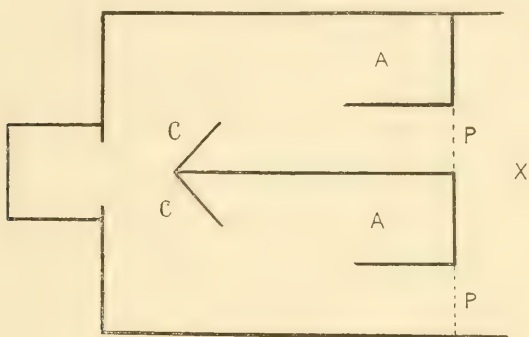
The conclusion, therefore, was that for this particular kind of test there was no preference for the dark.

Green, blue and red glass covers were substituted first for the white glass, and then for the black glass covering the respective compartments, but in a large number of trials no preference was indicated.

¹ Dr. WATSON found with the white rat no preference for dark passages. *Animal Education*, p. 56.

Test XI. Means of Orientation.

It was hoped to determine more accurately the signs which the guinea pig uses to learn its way.



Text-figure 10.

At *c c* cards of different colors could be slipped into a frame. *A A* are blind alleys, and *p p* removable partitions of glass. *X* is the food.

Preliminary experiments were made to see whether the guinea pig tends to form a habit of going in a certain direction for food. If any preference were shown it was for the right hand path (Text-fig. 10.) A glass partition was then put at *p* on the left path. The right path was soon learned. The cards (white and red) at *c c* were interchanged. Not a particle of difference was noticeable in the action of the guinea pig. When the partition was put to the right side the guinea pig learned the left path in three trials, with numerous random movements.

Two guinea pigs were tested a large number of times in this way. For one a green card always indicated the side of the partition, and when the partition was changed the card was changed. With the other guinea pig several colors were tried. They almost invariably chose the path which had led to the food at the previous trial, regardless of the cards. Two guinea pigs, tried without any cards, did the same thing.

The apparatus was made of wire and glass, so that I could wash it after each trial and thus do away with any possible path odor.

I believe my series of experiments too limited to draw any conclusions as to the effect of any particular sign in the field of vision. My experiments lasted two months and were performed every other day, two trials being given each day.

It will be noticed that the experiment is borrowed from YERKES.¹ In a long series of experiments on frogs he came to the conclusion that the frog observes colored cards and modifies its actions accordingly.

Test XII. Efficiency of contact stimuli for following a path.

It was suggested by Mr. G. H. MEAD that the reactions of the guinea pig might be direct responses to immediate contact stimuli, and that a distant stimulus, e. g., a recollection of the path, was not responsible for the reaction. While it is difficult for me to conceive how random movements could be eliminated and a path followed accurately after two months, if the performance were merely in terms of direct response to immediate stimulus, nevertheless I welcomed the suggestion of testing the part played by contact sensations in the learning and recollection of the labyrinth.

The labyrinth of text-figure 6 was taken into the dark room. I used three animals which had never before been in the labyrinth but which were perfectly tame. As the conditions for all were the same, and this number was used only to obviate any error arising from individual variation (which proved to be unimportant). I shall give a typical series from one animal.

The labyrinth was first learned in the light (electric). Carrot, as usual, was the food stimulus. Smoked paper was not put on the floor. The tameness of the animals prevented long delays as in the first experiments, and their activity was like that in their home cages.

¹ *Harvard Psychological Studies*, Vol. I, pp. 589-594.

Aug. 10.	Time	1 min.	Was evidently accidental.
Aug. 12.	Time	3.166 min.	
Aug. 13.	Time	.83 min.	
Aug. 14.	Time	.21 min.	
Aug. 15.	Time	.783 min.	
Aug. 16.	Time	1.166 min.	
Aug. 17.	Time	2.33 min.	
Repeated.	Time	.264 min.	
Repeated.	Time	1.33 min.	
Aug. 18.	Time	.913 min.	
Repeated.	Time	.264 min.	

I then substituted the wooden box used in test IV (text-fig. 8) for the wire food box, and turned out the light, but a loud noise in the next room frightened the guinea pig, so that the experiment was discontinued.

Aug. 19. The room is again made perfectly dark, the wooden electric box in the labyrinth. Time 3 min.

The guinea pig knocked against the wire at *K* (text-fig. 6) which seems to suggest inaccuracy of contact sensations.

Repeated. Time 2 min.

The times are rather longer than in the light. I replaced the wire box in the labyrinth and arranged the lighting wire so that when the swinging door was pushed open it would make the current. The contact conditions were then exactly the same as those obtaining in the light.

Repeated. Time 2 min.

The wire *K* was pushed down, which had never happened in the light, and the guinea pig walked over it to get in.

Aug. 20.	Time	1 min.
Repeated.	Time	1.25 min.
Aug. 21.	Time	1.25 min.
Repeated.	Time	2.5 min.
Repeated.	Time	1.83 min.

The wire labyrinth was now learned since there were few random movements, and though the time was longer than in the light, there was the accuracy of movement showing familiarity with the turns to be made.

To test whether the successive steps of the path were recollected through immediate contact stimuli, it was necessary to change the character of the contact and leave all the other conditions the same. Only the first reaction after such a change

would have significance. Should the recollection of the path be due to successive tactual sensations we would anticipate confusion and a lengthening of the reaction time when the contact stimuli have been changed.

A labyrinth similar to the wire labyrinth in its proportions was constructed of cardboard. (The advantage of the darkness is now apparent, since the visual conditions were not modified. The cardboard used had been purposely left in the experimental cage when the latter was not in use, but even then the odor conditions may have been slightly different.) Holes were made in the cardboard food-box, and the door was swung from the top as usual. A black cloth was spread over the floor of the experimental cage to change still more the tactual conditions. The electric wire was attached to the door to make contact when the door should be pushed open. The guinea pig was then brought to the dark room.

Aug. 22.

Time 1.75 min.

In order to test whether this time was accidental another trial was given.

Repeated.

Time .75 min.

One would hesitate to lay much stress on the guinea pig's sense of touch in comparison, e. g., with that of the white rat, because of the difference in the vibrissae. While the white rat's vibrissae are long, motile, and extremely sensitive, those of the guinea pig are shorter, coarse, and are not continually in use. The hair of the guinea pig serves for a covering rather than for a sense organ. I made a number of experiments by touching various parts of guinea pigs which were quite wild. If great precaution be taken that the guinea pig shall see no movement, its hair can be touched lightly at any accessible spot on the body behind the head without causing a reaction. I never succeeded in touching any part of the face without being seen.

We have seen that there was no lengthening in the reaction time when the contact conditions are changed, therefore we infer that the path through a labyrinth is not learned solely, or even largely, in terms of tactual sensations

Conclusions from tests X, XI and XII.

I. There are no indications that the guinea pig prefers a dark passage, or any particular color of light.

II. A colored object in the visual field, if it be stationary, apparently has no significance in the recollection of the path to food.

III. Alterations in the tactual conditions of the environment, other conditions being as far as possible unchanged, cause neither increase in reaction time nor confusion of movement.

IV. Since neither odor, vision nor touch is alone of paramount importance, and since, when light is shut out, the odor of a previous path being at the same time impossible and tactual conditions being new, the recollection of a path remains accurate and unconfused, we conclude that the factors of greatest importance in recalling a path are the sensations of running and turning, and of other movements gone through during a previous trial. The innervations of these movements are no doubt especially significant.

V. Hearing, seeing, touching and smelling are all of them important in the reactions of the guinea pig.

Summary of Work with the Adult.

1. The guinea pig can learn problems the solution of which depends upon activity, but not those requiring ingenuity.

2. The path to food is found first by accident, but when it is once found, random movements are rapidly dropped out and the reaction becomes almost automatic, providing no outside disturbing factors enter.

3. Odor of food is a stimulus which induces reaction, but the time required to learn the path from an odor stimulus alone is longer than from stimuli affecting all the sense organs.

4. Experiments to determine the efficiency of a visual stimulus alone were negative.

5. Kinesthetic sensations are of great importance in the recollection of a path.



IV. Development of the Guinea Pig Compared with that of the White Rat.

GUINEA PIG.	WHITE RAT.
Weight: Varies greatly at birth. Av., female, 70.8 gr.; male, 70.1; Adult, 800.5; m., 776.1 gr. ¹	Av., 5 gr. at birth. Adult, female 200; male, 250 gr.
Senses: Eye functions fully at birth.	Opens 16 to 17 days.
Ear functions at birth.	Functions fully after 13th day.
Touch never very sensitive.	Sensitive around the mouth, otherwise dull.
Smell perfect at birth.	Sensitive at birth.
Taste perfect at birth.	Present, but no differentiation between pleasant and unpleasant.
Body: Thoroughly covered with fur; complete muscular development except the hind legs.	Naked, ill-developed, immature in form and musculature.
Nervous system: practically completely medullated.	No medullation at birth.
Spontaneous movements not numerous but strong at birth. On second day movements very numerous.	Movement very slight and weak at birth, and does not attain vigor until fifth day.
Coördination: imperfect for first three days but perfect thereafter.	The few movements attempted are coördinated, and after learning to crawl (from 4th day) coördination rapidly increased.
Random movements: increase in number from 2 to 8 days. About constant throughout maturity.	Increase in number and vigor from 4th to 6th or 7th day.

Psychical Development.

Instincts: almost fully functioning at birth.	Instinctive reactions are characteristic of life up to 12th day.
Memory: proved to be present at second day. Perfect at 3 days.	Develops soon after 10th day. Perfect at 19 days.
Psychical maturity: 3rd day.	23 to 27 days.

The data for the white rat are derived from the records of SMALL² and WATSON.³

¹ MINOT. Senescence and Rejuvenation, *Journ. Physiol.*, Vol. XII, p. 131.

² *Amer. Jour. Psychol.*, Vol. XI, pp. 80-100.

³ Animal Education, Chicago, 1903.

V. *The Psychic Life of the Guinea Pig Compared with that of the White Rat.*

The Use of the Senses.—With the white rat, in the search for food, the sense of smell is paramount.¹ Smell is by far the most necessary sense in the life economy. This sense does not play nearly so important a part with the guinea pig. It is an efficient sensation, but is apparently neither a definite nor a strong incitement to reaction.

As with the guinea pig, so with the rat, vision seems to function mainly for orientation. But the rapidity with which moving objects, especially those which cast a shadow, are seen indicates that the guinea pig uses his sense of sight to detect the approach of dangerous objects.

The noises most quickly reacted to are those indications of danger and other signals made by the guinea pigs themselves; and sounds associated with feeding time.

The most important senses with the guinea pig are the kinesthetic. We can almost say that the guinea pig does the greater part of its remembering in kinesthetic terms. WATSON suggests that the memory of a path by young rats is motor.² How prominent a feature of rat life motor reactions are has not been discovered by any experiments yet carried out.

Memory Processes —WATSON found that memory processes of the white rat are not present before the twelfth day (p. 63), but before the twenty-second day they have reached a development sufficient to enable the solution of problems conditioned chiefly upon activity (p. 73). Psychological maturity is reached at from twenty-three to twenty-seven days of age (p. 83).

The experiments upon which these conclusions are based are: (a) A simple labyrinth used to test the earliest appearance of memory of a path to the mother; (b) other more complex labyrinths, in the solution of which activity was mainly involved, with memory of the path chosen; (c) boxes with different methods of opening, involving a memory of more complex movements than merely those of following a path to food.

¹ Animal Education, p. 84.

² Loc. cit., p. 85, foot-note.

The obtaining of the food may have first occurred accidentally and the successful movements have been rapidly selected for retention by being "stamped in," or by the elimination of random movements not pleasurably emphasized; or an intelligent factor may have entered into the selection of movements once found to produce the desired result of obtaining food. At any rate, it was found that "No form of problem which the adult rat is capable of solving presents insurmountable difficulties to the rat of twenty-three days of age" (p. 84).

The guinea pig stands in complete contrast to the white rat. Though no experimental records of memory were obtained from the guinea pig during its first day, a simple path was learned upon the second day, and upon the third day the most complex problem was solved, being a complicated labyrinth.

No experiments were made with the rat to determine how early a complicated labyrinth could be learned, but WATSON's rats solved a simple labyrinth at nineteen days.

When the guinea pig has found his way through a labyrinth he has reached the end of his psychical powers. He cannot pull a latch nor push a bolt, he will not depress an inclined plane, he will not chew a string nor stamp his foot. All the ingenuity which the white rat acquires after he has solved the labyrinth is a *terra incognita* to the guinea pig who thus pays the penalty of his early maturity.

The experience of the white rat extends to strange combinations of wires and springs, and all the delightful surprises revealed by secret doors. But when the guinea pig has turned the proper number of corners his dinner must be waiting for him or he does not get it.

The rat at three days is just learning to crawl, has never seen an object and remembers nothing. The guinea pig at that age has triumphantly recalled a complex path, at the end of which he sits eating his well-deserved carrot.

At twenty-three days the rat is lifting latches neatly, and forming what HOBHOUSE calls "practical judgments" as to the value of an inclined plane in a situation at the center of which

is his food—a desired thing, an end. The guinea pig is still wearing out the floor of the same labyrinth.

Were we to anticipate our later work we would suggest that the significant contrasting features in the two animals are their nervous systems. In the one a mature nervous system is accompanied by psychical maturity; in the other, neural immaturity permits great psychical development.

PART II. THE CENTRAL NERVOUS SYSTEM OF THE GUINEA PIG.

Introduction.

The investigation of the central nervous system of the guinea pig has for its purpose the description of the conditions present at birth, and the changes in the medullation of fibers between birth and maturity.

When an adequate notion of the nervous system and its growth changes has been obtained, it will be desirable to correlate these facts with the physical and psychical responses described in a previous part of this work. In view of the corresponding investigation of the white rat, a comparison will be made between the nervous system of the guinea pig and that of the white rat.

The progressive medullation of the central nervous system has been correlated by many authors with the progressive acquisition of function.¹ Nevertheless, WATSON has shown in the case of the white rat² that both the peripheral and the central nervous systems are entirely without medullated fibers at birth, while many impulses are at that time transmitted to the central system and there coördinated; and that complex associative processes are present before the medullation of those areas which may mediate associations in the cortex. Furthermore,

¹ A summary of the previous work on medullation will be found on pages 108 to 111 of *Animal Education*. The discussion of FLECHSIG's work is on pages 6 and 7, and a criticism of his wholesale correlations between function and medullation on pages 121-122.

² *Animal Education*, p. 117.

the complexity in the psychical life of the white rat is wholly out of proportion to the very few tangential fibers to be found in the cortex.

Technique.

The guinea pigs used for histological study were of the common English variety. From a large number of nervous systems hardened and stained the following ages were selected for examination :

Birth,	male,	108 grams,	used for illustration.
3 hrs.,	"	101.5	"
1 day,	"	84.5	"
2 days,	female	83	"
3 days,	"	106	"
3.5 days,	"	87	"
6 days,	"	70	"
11 days,	"	176.4	"
30 days,	"	250.4†	" used for illustration.
Adult,	male,	617.9	" used for illustration.

Each guinea pig chosen for study was in good physical condition, the wide range of weight indicated in the table being within the bounds of normal individual variation. Most of those animals used in the psychological experiments were afterward killed for examination.

The central nervous system was exposed and hardened *in situ* in MÜLLER's fluid. The tissue was kept in the dark during the hardening process, which required about fifty days for the small animals, and from sixty to seventy days for the adults. The sections were embedded in celloidin, ten grades being used,¹ and were cut 21 μ thick. They were stained according to the PAL-WEIGERT haematoxylin method, modified slightly to obtain the best results from this particular tissue. In detail the modified method is as follows: After cutting sections in 70% alcohol they were run to distilled water, then mordanted in MÜLLER's fluid 24 hours, at a temperature of 36 to 40° C. Washed thoroughly in distilled water, 2 to 4 hrs. Fresh WEIGERT's haematoxylin (cold) was poured over them, and they

¹ HARDESTY: Neurological Technique, p. 69.

were placed in a temperature of 40° C, 24 hrs. Washed well in numerous changes of tap water about 12 hrs. In differentiating no attempt was made to complete the permanganate decolorization at once, but the sections were allowed to remain in the permanganate from 15-25 secs., washed in distilled water, then placed in the oxalic-acid-sulphite mixture for several minutes, or until differentiation ceased to be apparent. Then they were washed in distilled water, replaced in permanganate a short time and the former process repeated. The best results were obtained when the tissues were carried back and forth three or four times. Subsequent washing in tap water was very thorough.

The sections of the spinal cord were made at the level of (1) the sixth cervical nerve roots and ganglia; (2) the eighth thoracic nerve roots; and (3) the third lumbar nerve roots. The levels were chosen thus in order that the sections might pass through the largest parts of the cervical and lumbar intumescensiae, and through the smallest region of the thoracic cord.

Sections of the encephalon were made (1) transversely, perpendicular to the base of the brain in front of the infundibulum and behind the optic chiasm, being located accurately by means of the tracts of the thalami; and (2) in the case of the cerebellum, sagittally, through the vermis.

Three ages have been chosen for reproduction, and drawings made with the help of a camera lucida. The magnification of the half tones of the cord is $21\frac{3}{4}$ diameters; of the encephalon, $9\frac{1}{2}$ diameters.

I. Description of Transverse Sections Through the Medulla Spinalis of the Guinea Pig at Birth.

Cervical Level.

A section through the cervical level at birth is reproduced in fig. 1, plate V. Reference to this figure will show that at birth a large number of fibers are medullated, and that the whole area of the white substance is almost uniform in its coloration. The gray substance is traversed by a large number of medullated fibers running in all directions.

The dorsal funiculus is subdivided into the fasciculus cuneatus and fasciculus gracilis, and the latter is again subdivided into two fasciculi by a clearly marked septum. A similar subdivision was found in the medulla spinalis of the white rat.¹ As in the white rat so in the guinea pig the fasciculus is very late in medullating. In the guinea pig this fasciculus presents an area considerably lighter than the substance immediately surrounding it, the medullated fibers in it being both small and comparatively few. In the fasciculus cuneatus a tongue of heavily medullated fibers passes from the level of the tip of the fasciculus gracilis down the septum posterior medianus to the commissura posterior (alba). On either side of the ventral portion of this tongue is a light oval area bounded laterally by the cervix columnae dorsalis, and extending from the commissura posterior to the substantia gelatinosa (fig. 1, plate V). This is the locality of the pyramidal tract.

A third area slightly lighter than the rest of the white substance is to be found in the lateral funiculus just ventro-lateral to the lateral apex of the substantia gelatinosa. Possibly there are in this locality some pyramidal fibers also.

In the cervical cord of the guinea pig at birth there are, then, three light areas: (1) the fasciculus gracilis; (2) the pyramidal area in the fasciculus cuneatus along the boundary of the cervix; and (3) an area containing a few fibers, around the lateral border of the apex of the dorsal column.

In the cervical cord the portion of the white substance immediately surrounding the gray substance is much darker than the white substance at the periphery of the cord, as is indicated in the figures. This appearance is due to two factors, (a) the great number of fibers passing between the ventral columns and the white substance, these fibers seeming to radiate from the ventral columns like spokes from a hub; (b) numerous fibers following the border of the gray substance; e. g., the fibers of the anterior commissure do not all pass directly to the cells of the gray substance, but have to wind in and out about the edge

¹ *Animal Education*, p. 94.

before they can effect an entrance. A further cause of darkening in the ground bundles around the margin of the gray substance may be that the longitudinal bundles are there more dense. In other words, in the section there may be more transversely cut fibers in the ground bundles than in the peripheral white substance. An enumeration of the fibers shows that in a given area there are in the lateral funiculus 16.7% more cross sections of fibers close to the ventral column than at the periphery. In the ventral funiculus the difference is 20.2% in favor of the given area close to the ventral column as opposed to a peripheral area in the same funiculus.

Thoracic Level.

At the thoracic level the lightly medullated area in the fasciculus cuneatus at the postero-lateral margin of the cervix columnae dorsalis (the pyramidal tract) is less well medullated than in the cervical region. It extends further toward the median line, so that in its ventral half it approaches nearer the median septum and extends ventrally as far as the commissura posterior.

The light area ventral to the lateral tip of the substantia gelatinosa appears in the thoracic segments. The fasciculus gracilis shows the two subdivisions commented upon in the description of the cervical level, the dorso-medial being the less well medullated.

In the thoracic as in the cervical cord the number of medullated fibers in the gray substance is worthy of attention.

Lumbar Level.

The light area in the funiculus cuneatus of the lumbar level occupies a position corresponding to that noticed in the section of the cervical, i. e., an oval area following the border of the cervix of the dorsal column, from the edge of the substantia gelatinosa to the commissura posterior, but separated from the latter by a well marked area of medullated fibers. This area is somewhat smaller than the corresponding area in the cervical, and contains a larger number of scattered medullated fibers than appear at the levels above it.

The light area ventral to the lateral tip of the substantia gelatinosa is present in the lumbar region, and corresponds to the similar area of the higher levels.

At the lumbar level the fasciculus gracilis does not appear in the section, and the funiculi dorsales are depressed below the level of the dorsal column on either side.

In all levels of the spinal cord there is a large amount of medullation, numerous well medullated fibers of all classes being present. Throughout the gray substance everywhere there are fibers passing in every direction, both large and small, separate and grouped into heavy bundles. Commissural fibers cross the median line on both sides of the canalis centralis, the most conspicuous commissure being the anterior. Here fibers running in the plane of the section are extremely abundant. They pass among many cross sections of fibers. Two bundles are enclosed by these commissural fibers (fig. 3, plate V, *y*), and are to be found in this position at all levels and in all individuals examined.

Small bundles of fine fibers are seen passing longitudinally at the junction of the cervix and caput of the dorsal column (fig. 1, Plate V, *x*). They constitute a part of a very extensive reticular formation which in this region passes through one-half or two-thirds of the cervix. The processus reticularis is well marked in the lateral region of the gray substance at every level.

1. In summarizing the appearances in the medulla spinalis of the guinea pig at birth emphasis is to be laid upon (1) the three partially medullated areas in the cervical and thoracic levels, to be found (a) in the fasciculus gracilis, (b) at the ventral border of the fasciculus cuneatus (the pyramidal tract), and (c) at the ventral margin of the apex of the dorsal column; (2) the two partially medullated areas in the lumbar cord, (a) the pyramidal tract which is less well marked than at higher levels, and (b) the area ventro-lateral to the substantia gelatinosa. The fasciculus gracilis is not present in the lumbar cord.

2. In transverse sections the peripheral third of the white substance does not appear to contain so many medullated fibers

as are to be found near the margins of the ventral columns.

3. At all levels there are many medullated fibers passing in every direction throughout the gray substance.

II. Development of the Medulla Spinalis from Birth to Maturity.

Cervical Level.

Between birth and the third or fourth days the formation of medullary substance in the medulla spinalis is apparently at a standstill. After the third day the light areas which have just been described, show a rapid darkening, so that before the eleventh day the medullation of the whole section has become practically uniform, the light areas being closely packed with medullated fibers. These fibers appear to have a smaller average diameter than the fibers of the neighboring funiculi, but their number is sufficient to render these areas as dark as those about them. Between eleven and thirty days the only noticeable change, besides increase in the area of the whole transverse section, is the still further darkening of the areas a, b and c.

In order to compare the white rat of thirty-five days with a guinea pig at approximately the same stage of development (thirty days), the transverse sections from the three levels of a thirty-day guinea pig are reproduced (figs. 5, 6, 7, plate V).

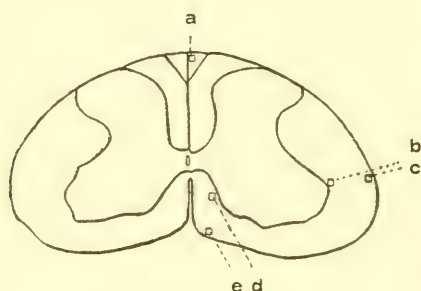
Upon reference to the figure of the cervical level it will be seen that the whole field has become darker than at birth by the great increase in number and in size of medullated fibers. The gray substance is traversed by a relatively larger number of fibers than is present at birth. The drawing of the thirty-day cervical section shows particularly well the cork-screw arrangement of the intra-medullary portion of the fibers passing into the gray substance from the zone of entering roots.

A small light area is to be found in the thirty-day cord also, at the ventro-lateral tip of the substantia gelatinosa. About the tip of the substantia gelatinosa are many fibers running in the plane of the section.

In the cervical cord of the adult (fig. 8, Plate V) the number of medullated fibers is largely increased, the white substance appearing nearly black. Throughout the entire section

the white matter adjacent to the gray appears darker than at the periphery of the section. That this darkening is not due wholly to mere enlargement of fibers already medullated at thirty days is inferred from the presence of small fibers in all parts of the cord.

In order to determine in how far new medullated fibers were responsible for these appearances a tentative enumeration of the fibers in several areas of the cervical cord was made. The areas chosen are represented diagrammatically in text-figure 11 below.



Text-figure 11.

Diagram of the cervical cord indicating the areas in which an enumeration of fibers was made.

In comparing the enumeration of these fibers in the adult with an enumeration in similar regions of the young at birth we find that in the adult there has been both a slight increase in the number of fibers and a considerable increase in their average diameter. The following table presents evidence of increase in number of fibers in the given areas between birth and maturity. The standard area within which the fibers were counted contained .00366 sq. mm., i. e., it was .06048 mm. on a side.

TABLE SHOWING NUMBER OF FIBERS IN GIVEN AREAS OF THE CERVICAL CORD AT BIRTH AND AT MATURITY.

	Dorsal funiculus.	Lateral fun.	Ventral fun.
At birth,	301	215.5 ²	218 ²
Adult,	408	203 ²	246 ²

² Average of enumeration at periphery and at margin of ventral column.

It will be seen that the total increase in number of fibers, all the funiculi being considered together, is 16.81%. The increase in number of fibers, then, can only partially account for the enlargement of the cord during this period.

In the adult the fasciculus gracilis is notably darker than the adjacent areas, whereas it was previously somewhat lighter. Similarly there is a corresponding darkening in the pyramidal area. The areas have been darkening by a great increase in number of medullated fibers. A count of the fibers in a given area of the fasciculus gracilis of both the adult and newborn shows that there has been an increase of 35.5% of medullated fibers in the older animal. In the newborn many fibers were too small to contribute to the darkening of the light areas.

Casual inspection shows that the fibers in the ventral funiculi are much larger than those of the dorsal fasciculi; this leads us to the conclusion that the number of fibers per unit of area is greater in the dorsal funiculus than in the ventral funiculus, and a count proves this to be the case. That is, those regions which show the smallest number of medullated fibers in early life ultimately possess a greater number of fibers than tracts which at that time are practically complete.

In the lateral funiculus there are somewhat fewer cross sections of fibers at the periphery than in the ground bundle near the ventral column, the ratio being 1:1.22. In the ventral funiculus it is found, likewise, that at the periphery there are fewer fibers than near the ventral column, the ratio being here 1:1.69. In both the lateral and the ventral funiculi the fibers at the periphery are larger than those near the gray substance.

Thoracic Level.

Little if any change occurs in the thoracic cord before the fourth day, as was found to be true also in the case of the cervical. The section at the sixth day shows much greater uniformity of medullation, and at eleven days the pyramidal tract can not be distinguished from the neighboring white substance. At eleven days also the fasciculus gracilis is becoming darker than the surrounding regions. In the fasciculus gracilis at

thirty days the medullation is much heavier, and in the adult it appears as dark as the corresponding area at the cervical level.

As at the cervical level, the white matter is darker at the border of the gray substance than at the periphery.

Lumbar Level.

The light area noted in the fasciculus cuneatus of the lumbar level does not disappear quite so completely as the corresponding areas of the more cephalic levels of the cord. By the sixth day the medio-ventral part has become evenly medullated, but at the eleventh day there is still an area in which there has been little or no increase in medullation. Notwithstanding the fact that in the lumbar level this light area was at birth very faintly marked, a suggestion of it persists here longer than in the levels above. Even at thirty days it is not quite lost in the general increase of medullary substance.

The fasciculus gracilis does not appear in the lumbar cord of thirty days, the dorsal funiculi being depressed in such a way as to form a groove at this region. Numerous fibers in the entering root zone and in the fasciculus cuneatus have made this groove relatively less deep than at birth. At maturity this depression can still be detected; and the fasciculus gracilis, though comparatively very small, appears at this level.

In the lumbar cord the crowding of the fibers in the ground bundle of the lateral and the ventral funiculi is not so conspicuous as it has been higher up. Fibers radiating from the ventral columns appear to be quite as numerous, but the longitudinally coursing fibers are probably not so numerous.

Summary of Changes in Medullation of the Medulla Spinalis Between Birth and Maturity.

1. In the cervical and thoracic levels three areas in the white substance are at birth noticeably lacking in medullated fibers:

- a) the fasciculus gracilis,
- b) the pyramidal area in the fasciculus cuneatus,
- c) in the lateral funiculus an ill-defined area ventro-lateral to the substantia gelatinosa.

2. Before eleven days the first two areas are medullated uniformly with the surrounding regions. The area in the lateral funiculus has received many new fibers and can be distinguished only as a narrow light zone bordering upon the lateral apex of the substantia gelatinosa.

3. By thirty days the two areas in the dorsal funiculus just distinguished as medullating late have become darker than the surrounding region. In the adult these areas are relatively still darker than at thirty days.

4. In the adult the light area in the lateral funiculus still has small fibers, many of which pass longitudinally within the limits of the substantia gelatinosa itself.

5. Since the lumbar level at birth does not possess a fasciculus gracilis it lacks one light area mentioned for the levels above. The other two light areas are present, though less well marked than at the higher levels.

6. The ventral half of the pyramidal area soon becomes well medullated, but its dorsal half remains poorly medullated for a longer time than at the higher levels, since even at thirty days it is still a little lighter than the adjacent white substance.

7. On the whole the cord of the guinea pig at birth is very well medullated in all its regions.

Increase in Area of Cross Sections of the Medulla Spinalis from Birth to Maturity.

The changes in the spinal cord which have been described above are such as are apparent by inspection of the various funiculi represented in the drawings. Contemporaneous with the darkening of the section by the increase in the size and the number of medullated fibers there has been an enlargement of the total area of the cord.

A selection of typical sections was made, and their transverse areas ascertained with the planimeter. The results are indicated in the following table :



TABLE I.

Table showing the increase in area of cross sections of the spinal cord of the guinea pig from birth to maturity.

Weight, grms.	Age,	Level,	Substance.		Total.
			White,	Gray,	
108	birth	Cerv.	2.88 sq. mm.	2.34 sq. mm.	5.22 sq. mm.
		Thor.	1.75	.84	2.59
		Lumb.	1.42	1.38	2.80
106	3 days	Cerv.	2.90	2.47	5.37
		Thor.	1.34	.85	2.19
		Lumb.	2.01	2.02	4.03
250.41	30 days	Cerv.	3.67	2.16	5.83
		Thor.	2.21	.93	3.14
		Lumb.	3.12	2.93	6.05
617.9	adult	Cerv.	6.90	2.69	9.68
		Thor.	4.76	.94	5.70
		Lumb.	5.80	3.07	8.87

The percentage increase in the white and gray substances and in the total area of the cross sections in the entire cord is graphically shown in the following table :

TABLE II.

The percentage increase in cross sections of the white substance from birth to maturity.

Age	Cerv.	Thor.	Lumb.
Birth	100	100	100
Adult	138.81	172	308.4

The percentage increase in cross sections of the gray substance from birth to maturity.

Age	Cerv.	Thor.	Lumb.
Birth	100	100	100
Adult	14.9	11.0	122.9

The percentage increase in total area of cross sections of the cord from birth to maturity.

Age	Cerv.	Thor.	Lumb.
Birth	100	100	100
3 days	2.8	15	43.9
30 days	11.6	21.2	116.0
Adult	85.4	120.08	216.78

It will be seen that the percentage increase in both the gray and white substance is much greater at the lumbar level than at the levels above, the lumbar cord, therefore, showing the greatest amount of developmental change from birth to maturity.

The progress of medullation in the thirty day guinea pig has attained about the stage reached by a thirty-five day white rat. The table below compares the areas of the spinal cords of the two animals.

TABLE III.

Table showing the areas of the cross sections of the spinal cords of a guinea pig thirty days old, and of a white rat thirty-five days old.

Animal,	Age,	Level,	White,	Gray,	Total.
Guinea pig	30 days	Cerv.	3.67	2.16	5.83
		Thor.	2.21	.93	3.14
		Lumb.	3.12	2.93	6.05
White rat	35 days	Cerv.	3.83	3.67	7.50
		Thor.	2.08	1.18	3.26
		Lumb.	2.41	4.07	6.48

It will be seen that the absolute areas are closely comparable, the cervical cord of the white rat being, however, larger than that of the guinea pig; so that in volume of the spinal cord as well as in the stage of medullation the guinea pig of thirty days may be compared with the white rat of thirty-five days.

To repeat what has been said before, by way of summary, the spinal cord of the guinea pig increases in area by the development of new fibers, and by the growth of fibers already formed at birth. When we see how heavily medullated the adult cord is, and know how much it has increased in area we conclude that there has been a very great addition of substance by both of these methods.

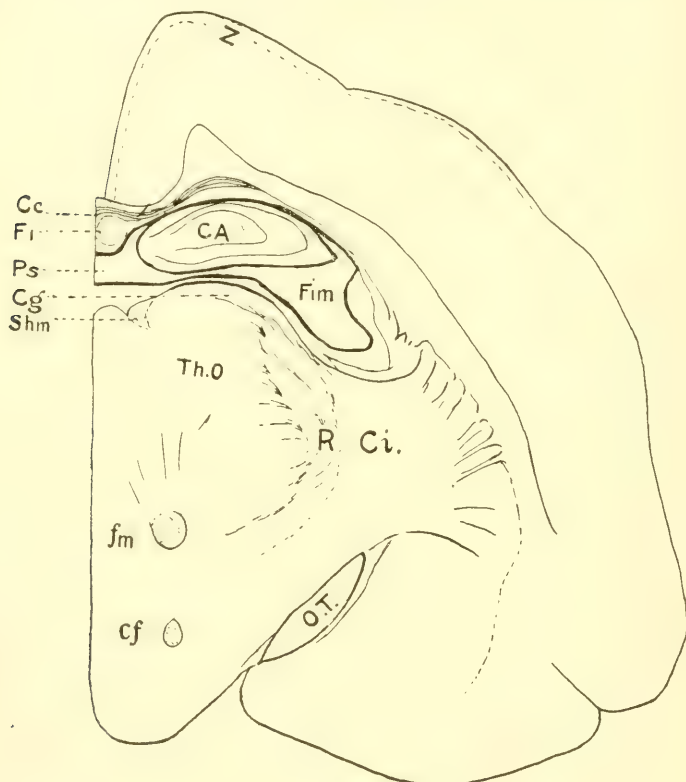
III. *The Encephalon of the Guinea Pig.*

Cerebrum.

In the encephalon at different ages the relation of the parts is not the same, so that it is impossible to get exactly comparable sections, and structures in the optic thalami were chosen

as being the most reliable marks for the determination of similar levels.

At birth the cerebral hemispheres show many well-medulated tracts. The section reproduced in figure 14, plate VI, is through the cornu Ammonis, ventral to which lie the thalamic structures. An outline drawing has been introduced (Text-



Text-figure 12.

fig. 12) as a key to the representations of the sections of the cerebral hemisphere. The letters in parenthesis refer to corresponding figures in the diagram.

In the diencephalon the thalamus opticus (*Th. o*) with fibers (*Radiatio lateralis thalami, R*) radiating into the internal capsule (*Capsula interna, Ci*); the fasciculus of Vicq d'Azyr (*fasciculus thalamo-mammillaris, Fm*); the Columna fornix (*Cf*);

and the lateral geniculate body (*Corpus geniculatum laterale*, *Cg*) appear as prominent features. The principal fiber tracts are already medullated.

As in other rodents in which the olfactory apparatus is well developed, the Ammon's horn (*Cornu Ammonis*, *CA*) is a conspicuous structure. In the guinea pig at birth the fibers of the Ammon's horn have only begun to be medullated in delicate layers separated by large areas of cells and unmedullated fibers. At the tip of the Ammon's horn the fimbria is already darkly medullated. Dorsal to the Psalterium (*Ps*) and immediately ventral to the Corpus callosum (*Cc*) is seen a group of fibers belonging to the Fornix longus (*Fl*).

Extending from near the median line dorsal to the fornix around the cortex and ventro-lateral to the lenticular nuclei is a dark mass of fibers, the white substance of the hemispheres, from which already numerous radial bundles emerge, passing in the direction of the cortical cells.

Not only are fibers to be seen radiating toward the surface, but also there are many fibers in the deeper portions of the cortex running parallel to the cortical surface. By using a high power very fine fibers are visible in the zonal layer (*Z*). But with this magnification no fibers are to be seen at the margin of the cortex. In the white rat this system of fibers does not begin to medullate until after the forty-second day.

Development of the Cerebral Hemispheres.

The drawings of the encephalon at thirty days and at maturity show a gradual increase in number and complexity of pathways formed by medullated fibers. The most remarkable changes have been in the Ammon's horn (*CA*), in the Psalterium (*Ps*), in the internal capsule (*Ci*), and in the white substance of the hemispheres. The optic tract appears well medullated. The bundles of fibers radiating toward the cortical surface from the white substance of the hemisphere become more abundant between birth and maturity, and extend further toward the surface. The fibers of the stratum zonale become more evident and the layer becomes thicker. In general, there-

fore, the tracts of medullated fibers become more densely medullated in the older animals.

The area of the cross section of the encephalon has increased in size, and incipient sulci are distinctly more marked in the adult than in the newborn brain. At the temporal margin of the cortex a sulcus, scarcely indicated at birth, has become well marked in the course of development. The increase in size of the temporal lobe seems, as indicated in the drawings, not to have been a progressively symmetrical growth; up to thirty days the ventral portion has developed most, after that the ventro-lateral portion undergoes the greatest change.

Cerebellum.

The sections from which the drawings were made were taken in the median sagittal plane, passing therefore through the vermis. The changes in this part of the encephalon are readily appreciated from comparison of the drawings.

As to general contour, it will be seen that the folia are numerous at birth, and in the course of development become larger and more pronounced. The PURKINJE cell layer is marked in the drawings by a white line (the cells not staining by this method) separating the molecular and granular layers.

At birth the molecular layer is free from medullated fibers. The granular layer contains fibers radiating from the white laminae; these fibers are especially numerous at the apex of the laminae. In the granular layer very many fibers are seen running more or less parallel to the white laminae. Further out in the granular layer such fibers are shorter and finer. Almost all the fibers seem to be medullated in the white laminae even at birth, and are densely packed together.

There is a great increase in the number of fibers found in the granular layer from birth to maturity. Such an increase is particularly marked in the fibers at the junction of the laminae and granular layer. It can be seen that the folia, present at birth and reaching the surface of the vermis, tend to divide as the animal becomes older, and that the folia deep-seated at birth push their way towards the surface.

The changes in the encephalon between birth and maturity as exhibited in the figures may be recapitulated as follows:

I. At birth no important cerebral pathways are unmedullated.

II. The number of fibers increases very greatly up to maturity.

III. The Ammon's horn corresponds in its development to the cortex, and at birth has very few medullated fibers.

IV. Few tangential fibers of the zonal layer are present at birth, and at no time are such fibers numerous in the stratum zonale of the guinea pig.

Increase in Area of Cross Sections of the Encephalon.

There are no observations showing the increase in weight of the encephalon of guinea pigs between birth and maturity. Linear measurements, however, show clearly that during this period the encephalon increases in size as well as in number of fibers.

The area of the cross sections used for illustration, of both cerebrum and cerebellum was measured, and is presented in the following table:

TABLE IV.

Table showing the increase in area of cross sections of the encephalon between birth and maturity.

Age,	One cerebral hemisphere,	Cerebellum (mesial section of vermis).
Birth	60.73	30.89
30 days	73.52	45.29
Adult	83.05	58.70

TABLE V.

Table showing percentage increase in area of cross sections of encephalon between birth and maturity.

Age,	Cerebral hemisphere,	Cerebellum.
Birth	100	100
30 days	21.06	45.15
Adult	36.77	90.03

IV. Comparison Between the Nervous System of the Guinea Pig and that of the White Rat.

At the end of the study upon the psychical processes of the guinea pig a comparison is made between the psychical and physical development of the guinea pig and the white rat. It was found that the white rat is born extremely helpless and undeveloped, whereas the guinea pig is independent and well developed. On the psychical side the guinea pig has reached the limit of his possibilities by the third day, while the white rat reaches psychical maturity from twenty-three to twenty-seven days. It was suggested that the contrast between the nervous systems of the guinea pig and of the white rat might be analogous to the contrast in their physical and psychical development.

We have seen in detail what is the condition of the guinea pig's nervous system at birth, and what changes occur during progress to maturity.

A description of the same cycle for the white rat will be found in *Animal Education*, pp. 87-111. Summarizing these results we find that in the white rat there are no medullated fibers present at birth; that in the spinal cord certain tracts (pyramidal tracts, fasciculus gracilis, etc.) medullate slowly, and that even in the adult the pyramidal tracts do not stain completely; that development in the cerebellum is more rapid than in the cerebrum; that medullation in many regions of the cerebrum is very slow up to the twenty-fourth day, after which the fibers rapidly mature.

Now, if we compare the sections of the guinea pig's spinal cord with sections of the white rat's spinal cord we see that the guinea pig at birth has reached the same stage of development attained by the white rat at twenty-four days. Similarity between the new-born guinea pig's psychical processes and those of the twenty-four day white rat is correlated with surprising accuracy with the similarity in their nervous systems. The similarity is present in a less marked degree between the cerebral

cortices owing to the fact that medullation in the guinea pig appears to be more advanced.

Very little change occurs in the central nervous system during the first three days of the guinea pig's life. Medullation then increases quite steadily but slowly as compared with the white rat. When the white rat is thirty-five days old it has a neural development at the same stage as the thirty day guinea pig.

Our conclusion then is that the guinea pig is psychically mature soon after birth, and at that time has a well medullated nervous system; furthermore, the degree of development of the nervous system corresponds to that of the white rat at 23-27 days, or its period of psychical maturity.



FIG. 1. Cervical Cord. At birth.



FIG. 5. Cervical Cord. Thirty Days.



FIG. 8. Cervical Cord. Adult.

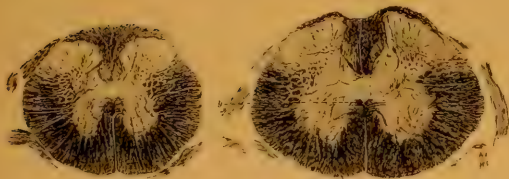


FIG. 2. Thoracic Cord. At birth.

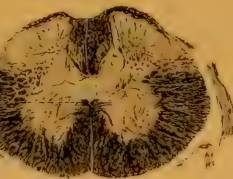


FIG. 3. Lumbar Cord. At birth.



FIG. 6. Thoracic Cord. Thirty Days.



FIG. 9. Thoracic Cord. Adult.



FIG. 4. Dorsal Column of Thoracic Cord. Thirty days.

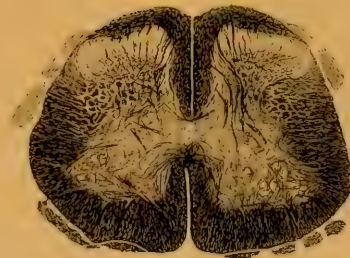


FIG. 7. Lumbar Cord. Thirty Days.

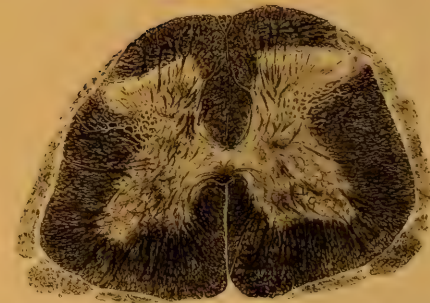


FIG. 10. Lumbar Cord. Adult.



FIG. 11. Vermis of Cerebellum. At birth.

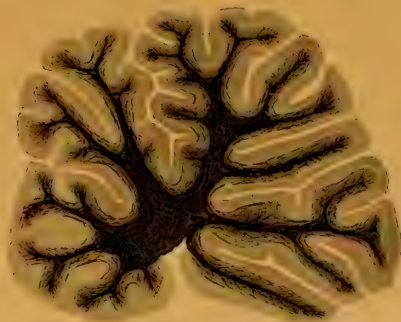


FIG. 13. Vermis of Cerebellum. Adult.



FIG. 12. Vermis of Cerebellum. Thirty days.

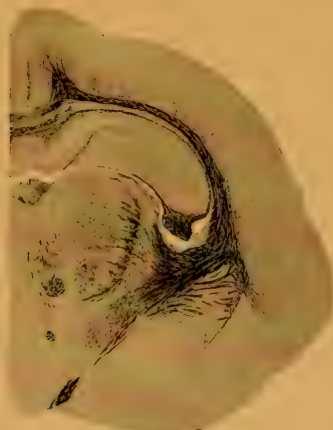


FIG. 14. Cerebral Hemisphere. At birth.

FIG. 15.
Cerebral
Hemisphere.
Thirty
days.

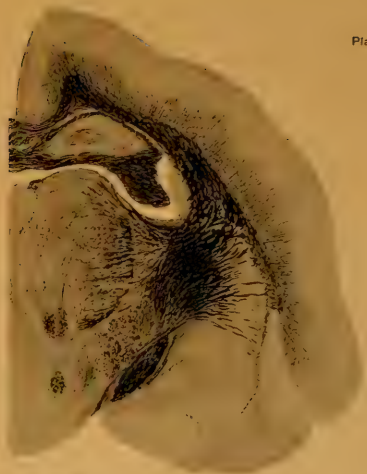


FIG. 16.
Cerebral
Hemisphere.
Adult.



EDITORIAL.

SOME UNEMPHASIZED ASPECTS OF COMPARATIVE PSYCHOLOGY.

We desire to enter a plea for a more detailed and extended study of what, for lack of a better term, we may call imitation in the mental processes of animals.

The word imitation is not used in any exact sense by writers on comparative psychology. KINNAMAN¹ and LLOYD MORGAN² have summarized the main facts covered by the word probably better than any of the other contemporary writers who deal exclusively with the mental processes of animals. They agree in the following classification of imitative behavior:

1. Mimicry which lies below the level of imitation.
2. Instinctive imitation, or automatic behavior.
3. Intelligent imitation:
 - a) of actions.
 - b) of results.

BALDWIN³ uses the terms "simple" and "persistent." Examples of these various types of imitation cannot be given here. We shall assume that every one is more or less familiar with them. In this paper the word imitation designates what MORGAN calls *intelligent imitation*.

THORNDIKE states emphatically that imitation in the above sense does not exist in animals lower than the primates. In the *Mental Life of Monkeys* (p. 42) he concludes: "Nothing in my experience with these animals then favors the hypothesis

¹ A. J. KINNAMAN. *Mental Life of Two Macacus Rhesus Monkeys in Captivity*, II. *American Journal of Psychology*, Vol. XIII, No. 2, p. 196.

² LLOYD MORGAN. *Habit and Instinct*, pp. 169-174.

³ *Mental Development*, p. 132.

that they have any general ability to learn to do things from seeing others do them." KINNAMAN in his *Studies of the Mental Life of Rhesus Monkeys in Captivity*, comes to a different conclusion: "Again, of the simple form as discussed by BALDWIN, I observed one very clear case. . . . This appears to me to come clearly under MORGAN'S class of intelligent imitation of an act. . . . There were many other cases of this type, as it seems to me, though they are more difficult to demonstrate. . . . But again I have observed two cases of imitation of the *persistent* and *intelligent* types. . . ."

SMALL¹ writes as follows: "My conclusions from all this experimental work, and from much other observation of rats is that they do imitate but that imitation with them is relatively simple. They imitate simple actions; but I have seen no case of what may, in lack of a better term, be called inferential imitation."

As far as our² observations have gone, we thoroughly agree with this conclusion of SMALL.

HOBHOUSE³, who is by far the most liberal interpreter of animal behavior, takes up no experiments which are especially designed to show this form of mental activity. He criticizes THORNDIKE very severely for denying outright that animals can learn by being put through an action. In fact he cites an experiment, conducted by himself, which is designed to prove the contrary (p. 148). In discussing imitation in animals lower than the primates (pp. 149-151), he says it remains uncertain whether they have the power of "reflective imitation"—imitation based on the perception of another's act and its result to that other. HOBHOUSE rightly insists that the possibility of a still simpler mental act must first be settled—"learning by the perception of an event and its consequence—when that consequence directly affects the learner." His "Experimental Results" (pp.

¹ WILLARD S. SMALL. *Experimental Studies of the Mental Processes of the Rat*. *American Journal of Psychology*, Vol. XI, No. 2, p. 162.

² JOHN B. WATSON. *Animal Education*.

³ HOBHOUSE. *Mind in Evolution*.

152-207) go to show that animals do learn by this perception of what the experimenter does, and its results. In the same section (pp. 207-5), he finally concludes that there is no natural tendency to learn by perception; still less by "reflective," as distinct from "simple" imitation. From this I gather that, while HOBHOUSE assumes that there is no *natural* tendency to imitate, still this mental act may be acquired in much the same way that habits of attention may be acquired by animals (p. 204). When on p. 259 he discusses "Articulate Ideas," he mentions a case of reflective imitation in the Rhesus monkey. He even puts it more strongly: "To transfer the act and apply it to himself and his own needs, was, at lowest, a strong case of reflective 'imitation.' But the use of the term imitation in this connection is really misleading. At most my act served as a hint."

Coming finally to PORTER's¹ excellent piece of work on the Psychology of the English Sparrow, we find this problem still untouched: "There is some proof of ability to profit by the experience of others, or of imitation. However, before any description of the real nature of this imitation can be given, additional and varied experiments are needed."

This short and incomplete survey of the field serves to show what inadequate experimental treatment this most important subject has had. That the subject is important, is evidenced by the fact that every investigator, at the end of the discussion of his results, mentions imitation. Yet few experiments have been especially designed to bring out the positive facts—if such there be. And no sane reader would deny utterly, on the basis of the few records we have, that animals can learn by imitation.

Most of us have been too busy, either in ascribing habit formations to lower and lower orders of animals, or in describing *the mental processes in general* in the higher animals, to give enough time and thought to a complete study of any one of the more typical mental acts. We are not criticizing any of the

¹ JAMES P. PORTER. A Preliminary Study of the Psychology of the English Sparrow. *American Journal of Psychology*, Vol. XV, p. 345.

experimental work here. Such work as has been done is abundantly necessary—the ground must be broken—but we do plead for long and careful studies in more restricted lines than that represented by simply taking an animal and watching its general behavior. It is time to put the animal in such situations that some one mental act may be exhibited to the exclusion of others.

JOHN B. WATSON.

LITERARY NOTICES.

Bethe, A. Allgemeine Anatomie und Physiologie des Nervensystems. *Leipzig, G. Thieme, 1903, pp. vii-485, 95 figs., 2 plates.*

This volume is a series of monographs on different phases of the same subject rather than a textbook of comparative neurology, as the substance of many of the chapters represents the author's own research. The first three chapters are devoted to a historical account of the structures of the nervous elements; and in the comparative description of the nervous system (chapters 4 and 5), the structure and relation of these elements is given a more prominent place than would be possible in a textbook.

In all forms possessing a nervous system the neurofibrillae are the essential nervous elements. The motor and sensory fibrillae of invertebrates are connected by networks in the ganglion cells, and are also continuous with each other in the neuropil. The nerve fibers of vertebrates are composed of strands of fibrillae imbedded in perinibrillar substance; at RANVIER's nodes the latter substance is interrupted, but the fibrillae are always continuous. Fibrillar networks are formed chiefly in the sensory ganglion cells; in most other cells the fibrillae pass directly through; they may enter by one dendrite and pass out by another without entering the neurite of the cell. BETHE maintains that motor and sensory fibrillae are put into direct connection by the "GOLGI nets" which envelop most of the central ganglion cells.

The peripheral networks of cells and non-medullated fibers are dealt with in chapters 6 and 7. The entire nervous system of the medusae is composed of these structures. They are also found in the integument, vascular system and digestive tract of mollusks, arthropods, worms and vertebrates. That these networks and not the muscles are the true conducting elements of the medusae is shown by the fact that two distinct bands of muscle may be made to contract by stimulating one of them. If the entire central nervous system of a gastropod mollusk is removed, stimulation of the body wall at one point will produce a general muscular response. In a similar manner the applica-

tion of a stimulus to the intestinal wall of the frog will produce contraction of the muscles of the stomach and oesophagus.

Chapter 8 gives a detailed account of the staining reactions of the nervous elements. NISSL's plates and the neurofibrillae owe their peculiar staining powers to two specific substances. The "NISSL substance" is soluble in aqueous solutions of HCl and ammonia; the "fibrillar substance" is soluble in acid alcohol and many of the ordinary fixing reagents. It may be fixed by corrosive sublimate and is insoluble in water, chloroform and ether. Good preparations of the fibrillae may therefore be obtained by fixing in ether and substituting ether for alcohol as a dehydrating reagent. Two methods of this kind are described. Centrosomes, intracellular canals, pigmentation, and changes in structure produced by poisons, or due to other abnormal conditions, are briefly discussed in chapter 9.

Nerve degeneration and regeneration form the subject matter of chapters 10-12. The first evidence of degeneration is the disappearance of the fibrillar substance and consequent loss of staining power. Degeneration is not necessarily due to the lack of continuity between fiber and cell but a wound which does not affect the conductivity of the fibrillae may produce degenerative changes. The conductivity of fibers may be interrupted by application of pressure or of injurious gases but degeneration will not ensue. The cutting of a peripheral nerve, however, may lead to the degeneration of both the central portion of the fiber and its ganglion cell.

After the lapse of two months or more the normal structure and functional activity of an isolated and degenerate peripheral nerve may be completely restored (auto-regeneration); if severed a second time the distal portion only will degenerate; but if the two ends of such an auto-degenerated nerve are grafted together, a union, both structurally and functionally perfect, will be established.

The peripheral nerves of the chick (chapter 13) are formed as chains of cells which may be observed before the processes of the neuroblasts within the spinal cord have become prominent. These chains of nerve cells differentiate from their substance the axis cylinders, and later become the sheath cells of the fibers. The dendrites of ganglion cells are also developed from a syncytium of nerve cells, and not as outgrowths of single neuroblasts.

The nature of nervous transmission is the subject of chapter 14. If by compression, the perifibrillar substance is practically eliminated from a certain portion of a fiber without injury to the neurofibrillae, the conductivity of the fiber is not affected. The neurofibrillae must,

then, be the conducting elements. When through degeneration, prolonged pressure, or the application of distilled water, a nerve fiber is rendered non-conductile, staining shows that the fibrillar substance has disappeared. Upon the removal of the abnormal conditions or upon the regeneration of a fiber, it is found that the return of functional activity is accompanied by the reappearance of the fibrillar substance. This substance is therefore connected with nervous transmission. A constant current of 0.05-0.2 milliamperes acting for 10 minutes upon a nerve will produce a polarization of the fibrillar substance and render the nerve non-conductile. If at once fixed and stained, that portion of the nerve near the anode will be much lighter, that portion near the kathode much darker than normal. If after polarization the fixation is delayed until the conductibility of the nerve returns, it will be stained with equal intensity throughout its course as in the case of normal fibers. The change which takes place during polarization is a chemical one. The fibrillar substance is set free at the anode and accumulates at the kathode. Darkly stained granules representing free fibrillar substance were observed at the anode among the fibrillae of the nerve. This chemical change takes place only in living and functional nerves and is therefore evidently a vital process essential to nervous transmission. According to BETHE the nervous impulse is produced by a chemico-physical process. A condition of increased affinity for the fibrillar substance passes wavelike along the fibrillae and the molecules of fibrillar substance are drawn toward the point of stimulation. Coincident with this chemical change, a negative electric current is produced. Either this current or the progressive movement of the fibrillar substance may be instrumental in transmitting the stimulus. BETHE believes that the chemical changes are of most importance in producing nervous impulses; the changes which take place are not oxidation processes, but merely fluctuations in the chemical affinity of the neurofibrillae.

Chapter 15 discusses the peculiar properties of the central nervous system, such as tonus, and inhibition of reflexes; on the ground of his well known experiment upon the brain of *Carcinus*, the author reasserts that both tonus and the transmission of reflexes are not dependent on the ganglion cells. In chapters 16-18 a review is given of the various phenomena characteristic of nervous reflexes. An interesting account of the effects of various poisons on the nerve elements follows (chapter 19). Most poisons affect first the elements of the central nervous system, because the fibers there are not protected by the thick sheaths which surround most peripheral fibers. Narcotics inhibit the

changes in affinity between the fibrillae and fibrillar substance; they therefore interfere seriously with nervous transmission. The state of increased sensitiveness to stimuli, which is one of the first symptoms of narcotic action, is due to the destruction of a substance peculiar to the elements of the central nervous system, which normally inhibits reflexes to a certain degree.

In chapter 20 it is shown that there are two types of muscle tonus. The tonus of striated muscle is due to the action of the central nervous system; in the case of certain non-striated muscles tonus is independent of the nervous system, and represents a state of rest. Such muscle passes into a state of tetanus when the central nervous system is removed (gastropod mollusks); the nervous system normally inhibits such a condition.

A brief review of the factors concerned in the inhibition of reflex action (chapter 21) is followed by a description in chapter 22 of the author's important work on the rhythmical contractions of muscle. It is shown that the number of respiratory movements in fishes is not regulated by the amount of O or CO₂ present in the water, but that if the sense organs of the mouth cavity are paralyzed by cocaine the movements will soon cease completely. The rhythmical muscular contractions during respiration are due to peripheral stimuli, not to a special power with which the muscle is endowed, nor to the influence of the cells of the central nervous system.

From the physiological standpoint the vertebrate heart and the bell of the medusa are very similar. If the sinus venosus of the heart, or the sense organs of the medusa are removed, rhythmical contractions cease, but in each case may be maintained by prolonged artificial stimulation; the contractions are true reflexes produced by definite stimuli. The transmission of the stimuli from the sinus venosus to the ventricle has been assumed to be a purely muscular function because the heart of the embryo chick begins to contract before the nervous structures have developed. BETHE points out that muscle fibers are not yet differentiated at this stage. The weightiest argument against the assumption of nervous transmission in the heart, is the slow rate of conduction (only 30 mm. per second in the frog). But BETHE shows that the rate of transmission in the dog's heart is about 300 mm. per second; also that if the muscle fibers of the atrium are rendered functionless by exposure to low temperature, or by the action of muskariin, stimulation of the atrium will cause contraction of the ventricle, although the muscle fibers of the atrium exhibit not the slightest reaction. It has been observed, too, that the apex of the ventricle often con-

tracts sooner than its base, and that a strip of heart muscle stimulated at one end may begin to respond first at the other extremity. All of the above facts point toward nervous transmission of definite stimuli. In the case of the medusae the stimuli originate in the sense organs of the bell; the source of the stimuli regulating the heart's action is practically unknown.

Following the text of the book is a valuable list of the recent literature on the nervous system. Much of the original work described by BETHE is necessarily incomplete, and as he himself states, the theories advanced are but preliminary, and will undoubtedly be subjected to future correction. They have already proved of value, however, in stimulating research along similar lines; and the many valuable results of the author serve to emphasize the importance of combining histological and physiological methods in attacking the abstruse problems of neurology.

C. W. P.

Goldschmidt, R. Ueber die sogenannten radiärgestreiften Ganglienzellen von *Ascaris*. *Biolog. Centrbl.*, Band XXIV, No. 5, pp. 173-182, 1904.

Discusses the radially striped ganglion cells of *Ascaris*. He finds them in all parts of the nervous system. The striped appearance is due to radial projections from the glia capsule extending into the cell for some distance, finally disappearing in the cytoplasm. He believes these to be characteristic of all ganglion cells and supposes the GOLGI nets of mammals to be of the same nature. They are probably not trophic. Their elastic nature may serve to suspend the cells in such a manner as to respond easily to vibrations. According to this supposition, a tearing of these projections is suggested as an explanation of the serious disturbance of the nervous system caused by severe mechanical shock.

G. WAGNER.

Kolmer, W. Eine Beobachtung über vitale Färbung bei *Corethra plumicornis* (Vorläufige Mittheilung). *Biolog. Centrbl.*, Band XXIV, No. 6, pp. 221-223, 1904.

Larvae kept for weeks in methylene blue solutions showed no staining. After feeding on *Stentor* killed with methylene blue, they showed staining of nervous elements. This staining appeared and disappeared at intervals. As the animal remained alive for many hours afterward, the staining was probable truly *intra vitam*.

G. WAGNER.

Coggi, A. Sviluppo dei organi di senso laterale, delle ampolle di Lorenzini, e loro nervi rispettivi in *Torpedo*. *Archivio Zoologico*, Vol. I, Fasc. 1, pp. 59-107, 1902.

A detailed discussion of the development of the lateral line and

Lorenzian ampullae and their nerve supply in *Torpedo*. The Lorenzian ampullae are homologous with the "terminal buds" of other authors. There are no "pit organs" in *Torpedo*. There is no genetic relation between the ampullae and the lateral line organs. There is no morphologic distinction between the lateral line and the organs of Savi. The latter are mere modifications of the former.

G. WAGNER.

Spitzka, Edward Anthony. Contributions to the Encephalic Anatomy of the Races. First Paper:—Three Eskimo Brains, from Smith's Sound. *The American Journal of Anatomy*, II, 1, pp. 25-71.

Well illustrated with figures of the different surfaces of the brains, with very full descriptions and measurements.

G. E. C.

Dexter, Franklin. The Development of the Paraphysis in the Common Fowl. *The American Journal of Anatomy*, II, 1, pp. 13-24.

The paraphysis first appears in the 6.7 mm. embryo, and persists in the adult.

G. E. C.

Hardesty, Irving. The Neuroglia of the Spinal Cord of the Elephant with some Preliminary Observations upon the Development of Neuroglia Fibers. *The American Journal of Anatomy*, II, 1, pp. 81-103.

The so-called "neuroglia cell" is a reduced syncytium, and the origin of the fibril is intrasyncytial rather than intracellular or intercellular.

G. E. C.

Bardeen, Charles Russell. The Growth and Histogenesis of the Cerebro-Spinal Nerves of Mammals. *The American Journal of Anatomy*, II, 2, pp. 231-258.

The author has employed the method of isolating the nerves in early embryonic stages and studying them in teased preparations. This procedure gives important data on structures the nature of which in section is more or less doubtful. The paper strongly supports the theory of His. The nerve fiber unites with the muscle before the development of the sarcolemma, which becomes so intimately fused with the sheath of SCHWANN that the boundary between the two structures is indistinguishable.

G. E. C.

Schlapp, M. G. The Microscopic Structure of Cortical Areas in Man and Some Mammals. *The American Journal of Anatomy*, II, 2, pp. 259-281.

A comparative study of functional centers according to structure and localization. Centers differ not so much in the characters of the individual cells as in the composition of the entire cortex of the regions.

G. E. C.

Streeter, George L. Anatomy of the Floor of the Fourth Ventricle. *The American Journal of Anatomy*, II, 3, pp. 299-314.

The topographical markings of the floor of the fourth ventricle

agree in the main with the descriptions by RETZIUS, but the author's studies are concerned with the significance of these markings in relation to the underlying structures of the medulla. G. E. C.

Mall, Franklin P. On the Transitory or Artificial Fissures in the Human Cerebrum. *The American Journal of Anatomy*, II, 3, pp. 333-340.

The fissures are produced by the disintegration of the walls of the brain vesicles. A table is compiled from over fifty brains to show the relation of different hardening agents, especially formalin and alcohol, to the occurrence of these fissures. G. E. C.

Mellus, E. Lindon. On a Hitherto Undescribed Nucleus Lateral to the Fasciculus Solitarius. *The American Journal of Anatomy*, II, 3, pp. 361-364.

In the dog this nucleus consists of "large, oval or pear-shaped cells" extending upward 2 mm. from the level of the calamus scriptorius. A corresponding group of smaller cells occurs in man.

G. E. C.

Holmgren, Emil. Einige Worte zu der Mitteilung von Kopsch: "Die Darstellung des Binnennetzes in spinalen Ganglienzellen und anderen Körperzellen mittels Osmiumsäure." *Anat. Anz.*, XXII, No. 17-18, pp. 374-381, Jan., 1903.

The author reviews and, in certain points, corrects KOPSCH's criticism of his work on intracellular canaliculi. By way of illustration he introduces two new figures, with descriptions, of the "Trophospongium" and Saftkanälchen in the nerve cells of birds.

G. E. C.

Holmgren, Emil. Ueber die sog. "intracellulären Fäden" der Nervenzellen von *Lophius piscatorius*. *Anat. Anz.*, XXIII, No. 2-3, pp. 37-49, April 8, 1903.

A review of the author's previous publications on the nerve cells of *Lophius* with special reference to SOLGER's paper on *Torpedo*. The author denies the existence of a pericellular lymph space normally, and abandons the idea that the intracellular fibrils are nervous.

G. E. C.

Wolff, Max. Ueber die Kontinuität des perifibrillären Neuroplasmas (Hyaloplasma, Leydig-Nansen). *Anat. Anz.*, XXIII, No. 1, pp. 20-27. March 17, 1903.

The finer structure of the axone terminals upon the muscle supports HELD's theory regarding the pericellular net of GOLGI, and affords a morphological basis for the LEYDIG-NANSEN theory of hyaloplasm.

G. E. C.

Kronthal, P. Zum Kapitel: Leucocyten und Nervenzellen. *Anat. Anz.*, XXII, No. 20-21, pp. 448-454, Jan. 30, 1903.

The author reviews his theory of the origin of the perikaryon and dendrites from leukocytes, with special reference to the GOLGI method, the histogenesis of the nerve, and the theory of FRAGNITO.

G. E. C.

Zuckerkindl, E. Die Rindenbündel des Alveus bei Beuteltieren. *Anat. Anz.*, XXIII, No. 2-3, pp. 49-60, April 8, 1903.

The dorsal part of the commissura superior receives fibers through the alveus from the pallium. It represents, therefore, the primitive corpus callosum.

G. E. C.

Zugmayer, Erich. Ueber Sinnesorgane an den Tentakeln des Genus *Caridium*. *Zeit. f. w. Zool.*, Bd. LXXVI, Heft 3, pp. 478-508, 1904.

Agabow, A. Ueber die Nerven der Sclera. *Archiv. f. mik. Anat.*, Bd. LXIII, Heft 4, pp. 701-709, 1904.

Kallius, E. Sehorgan. *Merkel u. Bonnet's Ergebnisse*. Bd. 12, (1902) pp. 348-441, 1903.

Kölliker, A. Die Entwicklung und Bedeutung des Glaskörpers. *Zeits. f. w. Zool.*, Bd. 76, H. 1, pp. 1-25, 1904.

Police, G. Sul sistema nervoso stomatogastrico dello Scorpione. *Archivio Zoologico*, Vol. I, Fasc. 2, pp. 179-198, 1903.

Meigs, E. B. On the Mechanism of the Contraction of Voluntary Muscle of the Frog. *Amer. Jour. Med. Sci.*, April, 1904.

Attention is called to the resemblance that muscle fibers in water rigor have to those in tetanus. In both instances the fibers assume a beaded appearance and since in water rigor the form is dependent upon the absorption of water, it is supposed that in tetanus a like absorption takes place. That contraction would result from this is demonstrated by an ingenious model consisting of a closed rubber tube attached to an air-pump and encircled at short intervals by metal rings; these are attached one to another by numerous longitudinal inelastic threads. When air is forced into the tube, the segments between pairs of rings become spherical and the inelastic threads change their form from straight to curved lines, thus shortening the fiber as whole.

Ingenious as this hypothesis is, it scarcely touches the real problems of muscle action. Why do muscle fibers at rest fail to take up fluid which they are supposed to absorb when stimulated and how does a contracted muscle ever relax? These and like questions that must arise in the mind of the reader, show at once the incompleteness of Dr. MEIGS' hypothesis and place it in unfavorable light in comparison with the older theories of muscle action such as those advanced by ENGELMANN and others.

G. H. P.

Härtl, J. Ueber den Einfluss von Wasser und anisotonischen Kochsalzlösungen auf die Grundfunctionen der Quergestreiften Muskelsubstanz und der motorischen Nerven. *Arch. f. (Anat. u.) Physiol.*, Jahrg., 1904, Heft. 1-2, pp. 65-93, 1904.

Motor nerves lose their irritability when placed in distilled water. This can be restored by placing the nerve for a time in hypertonic solution of NaCl (2-3%) and then bringing it back into 0.5% NaCl. Similarly, if the irritability has been destroyed by placing the nerve in a strong (hypertonic) NaCl solution, it can be restored in from one-half to two hours by immersing the preparation in a hypotonic solution of the same salt (0.2-0.3%).

R. P.

Gotch, F. The Time-Relation of the Photo-electric Change produced in the Eyeball of the Frog by Means of Colored Light. *Jour. Physiol.*, XXXI, No. 1, pp. 1-29, 1904.

The excised eyeball of the frog gives photo-electric responses when it is subjected to the influence of colored light, however obtained. These responses fail or become very feeble in the infra-red or infra-violet regions of the spectrum. The range of light vibrations eliciting photo-electric responses corresponds very closely with the range of vision in man's color sensations. The capillary electrometer gives records from which the time relation of the response to a given color may be determined. A response of the same general type as the illumination response is obtained when light is suddenly replaced by darkness. The excitatory process is of one fundamental type and is characterized electrically by a difference of potential between fundus and cornea of such character that a current flows through the eyeball from the former to the latter. There is a distinct difference in the latent periods of the response to different colored lights. The response to red light has the longest latent period (ca. 0.3 second); the violet light response has a shorter latent period (ca. 0.25 second); the latent period of the response to green light is the shortest (less than 0.2 second). The results are held to be in accordance with the YOUNG-HELMHOLTZ theory as modified by MAXWELL.

R. P.

Nagel, W. A. and Schaefer, K. L. Ueber das Verhalten Netzhautzapfen bei Dunkeladaptation des Auges. *Zeit. f. Psv. u. Phys. d. Sinnesorgane*, Bd. 34, pp. 271-285, 1904.

The results presented in this paper complement very prettily the work already done by PIPER. As is known, PIPER experimented upon the increase in the sensitivity of the larger retinal surfaces during the process of adaptation to darkness and found that, if the sensitivity of the retina adapted for light be compared with that of the retina thoroughly adapted for darkness, the ratio of increase is from 1:2000 to

1:9000. The explanation for this enormous increase in sensitivity is to be found in the lack of rods in the central region of the retina. The rods are used in weak light, while the cones are used in strong lights.

But it cannot be supposed that the stimulus threshold for the cones remains the same under all circumstances. Is not the sensitivity decreased by long activity and increased by rest? The difficulties in the way of a satisfactory answer to these questions are almost insurmountable. According to the authors, however, there are three possible methods of approach:

1. One can arrange a fixation mark of minimal size and bright enough to be securely above the foveal threshold. A steadfast fixation point is thus secured. This is very necessary since at the moment of the onset of adaptation for darkness the greater sensitivity of the peripheral portion of the retina causes one to fixate with the periphery rather than with the fovea.

2. One can make use of the fact that the adaptive increase in the sensitivity of the rod apparatus is least for pure red light; and is the smaller, the longer the wave length of the light. In consequence of this a foveal threshold can be determined without danger of the point of regard being turned towards the periphery.

3. Since it takes 5 minutes for the process of adaptation for darkness (after the eye has been adapted for light) to set in, it is possible, in the first few moments after entrance into the dark room, to obtain a foveal threshold without the fixation mark being diverted either to the paracentral or to the peripheral portion of the retina.

Summary of results obtained from all three methods.

A. Investigations with red light.

1. With foveal and paracentral region.

- a. When the adaptation for brightness is produced by strong artificial light, the increase in sensitivity during the first minute is about thirty-two fold. From the end of the first 30 seconds to the end of the sixth minute we have the ratio of 1:16.

- b. When the adaptation for brightness is produced by bright sunlight, the increase in sensitivity, from first moment of entrance into the dark room, to the onset of adaptation for darkness, is in the ratio of 1:200.

2. With the foveal region alone a fourfold increase in sensitivity is found.

B. Investigations with green and blue lights.

1. With the foveal region alone the increase in sensitivity is again fourfold.

2. With the foveal and paracentral regions quantitative experiments could not very well be made because the green and blue lights mixed with the white of the ideo-retinal light more easily than did the red light. Nevertheless, a marked increase in the sensitivity was found.

J. B. W.

Nagel, W. A. Einige Beobachtungen über die Wirkung des Druckes und des galvanischen Stromes auf das dunkleadaptierte Auge. (Zum Teil nach Versuchen von Herrn. cand. med. BLECKWENN). *Zeit. f. Psy. u. Phys. d. Sinnesorgane*, Bd. 34, pp. 285-291, 1904.

This contributor first confirms the results of G. E. MÜLLER, who has reported, in effect, that the sensitivity of the eyes for inadequate stimulation by the galvanic current is independent of the state of adaptation of the eyes. The author's next observations concern the differences in the behavior of the pressure phosphenes when the eye is adapted for light and when adapted for darkness. It was found, that with a given position of the eye, and with a definite pressure on the eyeball, the same form of pressure phosphene could be recalled again and again. Having chosen, with eye adapted for light, a definite phosphene as a standard (in this case a bright ring with one or two concentric rings inside of it) Professor NAGEL made some comparisons when the eye was adapted to darkness. The result was that the intensity of the pressure phosphene in the eye adapted to darkness was slightly increased. Qualitatively the appearance of the two phosphenes was very different. The ring in the eye adapted to the light was yellowish and small; in the eye adapted to the dark it was bluish-white and noticeably broadened.

Since the author is dichromatic (a greenish tone in yellow and a violet tone in blue could not be perceived), it occurred to him that the color of the phosphene seen in the eye adapted to the dark might be complimentary to the color of the phosphene seen in the eye adapted to the light. So he repeated the above experiment upon persons possessing normal color vision. They stated that the phosphene seen in the eye adapted to the light appeared yellowish, inclining to red; the phosphene seen in the eye adapted to the dark appeared bluish or bluish-white.

The author next tested the galvanic phosphenes in the eye adapted to the light and in the eye adapted to the darkness, to see if any difference in color could be found. The phosphenes produced in this way were always quantitatively and qualitatively alike in the two eyes.

Numerous experiments were then made to test whether the sensitivity of the eyes adapted to the darkness, is altered by the effect of an

electrical current passing through the eyes. A variation of the limen of the light stimulus was produced neither when the current flowed from the layer of nerve fibers to the layer of rods and cones, nor when the current flowed in the opposite direction.

Finally the author tested the effect of long continued pressure upon the visual process of adaptation for darkness. A threshold value was taken, (1) after 30 minutes in the dark room, (2) after wearing, for 30 minutes a light-tight bandage which exerted no pressure, and (3) after wearing a pressure bandage for 30 minutes. All three cases gave exactly the same threshold value.

J. B. W.

Abelsdorff, G. and Nagel, W. A. Ueber die Wahrnehmung der Blutbewegung in den Netzhautkapillaren. *Zeit. f. Psy. u. Phys. d. Sinnesorgane*, Bd. 34, pp. 291-300, 1904.

If one glances at the blue sky, one sees, as is well known, numerous small glittering particles moving in tortuous pathways across the field of view. The particles are in constant motion, and since they never pass the point of clearest vision, it is impossible clearly to make out their form. The phenomenon is in some way connected with the circulation of the blood in the retina. If one presses lightly with the finger against the eyeball, the regular and uniform movement of the particles changes to one of a pulsating character, while a stronger pressure brings the particles almost to a standstill. Then after the release of the pressure the particles hasten across the field of view even more rapidly than before. That the phenomenon is not produced by the mechanical stimulation of the elements sensitive to light by the blood cells which circulate in the capillaries is proved by the fact that it is wholly lacking in darkness and weak lights, and even in strong lights the phenomenon can be seen only when the stimulating lights possess wave lengths lying within definite boundaries.

Both RUETE and ROOD have mentioned this phenomenon and remarked that it can be best observed with the aid of blue glass. The present investigators finding, however, that the movement of the particles cannot be seen with the aid of any and every blue light jointly undertook to make a more thorough investigation of the conditions under which this phenomenon appears.

According to their view there are two possible ways of explaining the phenomenon: It may be a shadow phenomenon, similar to that of the vein-figures of PURKINJE, caused by the absorption of certain light rays by the blood corpuscles; or it may be a phenomenon of light refraction, since conceivably the red and white corpuscles, acting as lenses, might focus the light on the sensitive layer or the retina. The

authors throw the latter supposition out of court, since one can think of no way in which the corpuscles can act as lenses.

Accepting, then, light absorption as the more probable manner of explanation they begin their experiments. As light absorbing elements only the red corpuscles come into consideration. These strongly absorb the blue and violet rays in the spectrum. This explains why the phenomenon can be best observed in these lights, but since haemoglobin also absorbs the yellow green rays considerably one would expect to find the phenomenon visible, at least to some extent, in this light. At first the investigators were unable to do this, but after numerous experiments with many light filters composed of different kinds of light absorbing mixtures they were enabled to show that the phenomenon is visible in all lights that are absorbed in the spectrum of the haemoglobin.

The intensive absorption of the haemoglobin then for indigo, blue and violet explains in a satisfactory way the appearance of the shadows of the corpuscles in these lights; it explains why the shadows are so much more intensive in the violet-blue than in the yellow-green. On the other hand, the permeability of the haemoglobin for the cyan-blue, blue-green, red and orange harmonizes completely with the fact that in these lights the swarming of the corpuscles cannot be seen.

J. B. W.

Hall, G. Stanley and Theodate L. Smith. Reactions to Light and Darkness. *American Journal of Psychology*, Vol. 14, pp. 21-83, 1903.

This report is based on questionnaire returns obtained from two normal schools, two colored schools, and one school for the blind. White pupils in the fifth grade, from ten to twelve years old, contributed also. The ages of the normal students lay mostly between eighteen and twenty-two, while those of the colored students ranged from ten to twenty-eight. The investigation sought to discover the emotion reactions to darkness, dawn, twilight, artificial light, sudden transitions; and to learn the fancies connected with the sun, darkness, and light. No classification along lines of age or sex was attempted. As to race differences, the writers state that none specific occurred save those directly referable to degree of educational opportunity.

The results of importance follow: (1) Longings for dawn occur in 85% of 389 cases. Included are about 6% where a pleasurable event is anticipated. In the rest the character of the longing varies from mere restlessness to real light hunger. (2) Night fears occur in 73% of 389 cases. In about 11% of these the fear is of darkness itself. In the remainder it is of specific live objects, natural or supernatural. The most frequent fear is of being seized or grabbed at. About

6%, all adults and destitute of superstitious beliefs about darkness, still have these fears when in the dark or in a closed space. (3) Blind children dread the night and, if they are to go about, desire companions. The reaction here may be due to stillness or loneliness; and one person so reports. (4) Twilight hour is loved in 273 cases; shunned in 79, and indifferent in 32. Preference among whites was to be alone, while 80% of the returns for negroes showed desire for company. "The sentiments typical at sunset, given in order of their numerical importance, are moral and religious aspirations, sadness, loneliness, rest, awe and reverence, quiet and thoughtfulness, peace, gladness, regret, sorrow and longing." (5) Of 291 adults 197 had personal experience of the exhilarating effect of artificial light—results that agreed with observations upon 32 children. The amount of this effect varies from a slight increase in mental and physical activity to cases of actual abandon. No effect had been noticed by 62 adults. (6) Entering shade is followed by depression of spirit; entering sunlight rouses cheerful feeling. The blind are susceptible to these sudden changes, but not to the change from day to night. The direction of susceptibility is not stated. (7) The effects of a longer period of gloom appears in the poorer quality of mental work and its smaller quantity. So it seems to be with the blind. GREELY, the Arctic traveler, noted among his men insomnia, irritability, gloom, and indisposition to exertion as the winter wore on, leading to symptoms of mental disturbance even more serious. Thermal effects must not be forgotten though where these differed widely, as in STANLEY'S march through the great forest in Africa, this traveler noted similar reactions among his company, and the strong revulsion of feeling on passing its confines. (8) The following examples of children's phototropisms are frequently given: they play on the sunny side of the room or the street, disregard heat or cold to play in sunshine, babies creep toward the sun, children are always happier and more active in sunshine. (9) This reaction at times becomes negative, apparently under conditions of fatigue. A child tired and sleepy with play in the sun usually craves the opposite condition for sleep. Travelers in lands of brilliant sunshine often report this as becoming positively painful. Thermal effects here probably offer complications, though GREELY found insomnia and restlessness consequent upon the long Arctic day.

The richness of the fancies woven about light and darkness is taken as significant in favor of the theory of recapitulation. The value of such evidence ought to be questioned in view of the complicating effects of social heredity.

The general character of the evidence upon which this article is based is two-fold: reports of individuals about themselves and about others under their observation. Upon the second sort depend the chief facts in 6 to 9 above, and part of 5, as well as largely the facts about the blind. To what extent this evidence is memory generalized does not appear. Original data are given merely for illustration.

CHARLES T. BURNETT.

Zwaardemaker, H. Eine bis jetzt unbekannt gebliebene Eigenschaft des Geruchssinnes. *Arch. f. (Anat. u.) Physiol.*, Jahrg. 1904, Heft. 1-2, pp. 42-48, 1904.

Shows that if there is a periodical breaking of the air column *within* the nasal cavity (produced by alternate inspirations and expirations) an *intermittent* olfactory sensation results. If the air column is broken periodically *outside* the nasal cavity (i. e., in the olfactometer tube) a continuous olfactory sensation results.

R. P.

Cramer, W. On Protagon, Cholin and Neurin. *Jour. Physiol.*, XXXI, pp. 30-37, 1904.

Physiological chemistry of the brain.

R. P.

Zwaardemaker, H. und Quix, F. H. Ueber die Empfindlichkeit des menschlichen Ohres für Töne verschiedener Höhe. *Arch. f. (Anat. u.) Physiol.*, Jahrg. 1904, Heft. 1-2, pp. 25-42, 1904.

Muskens, L. J. J. Ueber eine eigenthümliche compensatorische Augenbewegung der Octopoden mit Bemerkungen über deren Zwangsbewegungen. *Arch. f. (Anat. u.) Physiol.*, Jahrg. 1904, Heft. 1-2, pp. 49-56, 1904.

Stuart, T. P. A. The Function of the Hyaloid Canal and some other New Points in the Mechanism of the Accommodation of the Eye for Distance. *Jour. Physiol.*, XXXI, pp. 38-48, 1904.

Delage, Y. Sur les mouvements de torsion de l'oeil. *Arch. d. zool. expér. et gen.* 4 ser., T. I, No. 3, pp. 261-306, 1903.

Smallwood, Mabel E. The Beach Flea: *Talorchestia longicornis*. *Cold Spring Harbor Monographs*, I, 27 pp., 3 pls., 3 text-figs. 1903.

With this monograph a series of publications from the Biological Laboratory of the Brooklyn Institute of Arts and Sciences at Cold Spring Harbor is begun in which special attention will be given to the natural history of the animals in the region of the station.

The present paper consists of an anatomical description of the beach flea, and an account of studies of its ethology. Breeding, moulting, habitat, burrowing, locomotion, phototropism, food and feeding, relation to water, and movements are in turn briefly considered in the light of observations made in nature or in the laboratory by the author. Review space does not permit the presentation of the facts of this in-

teresting paper, and it must therefore suffice to call attention to the importance, as a preparation for experimental work, of the study of an organism with respect to its habitat and behavior in its natural environment.

R. M. Y.

Wheeler, W. M. A Crustacean-eating Ant (*Leptogenys elongata* Buckley). *Biol. Bull.*, Vol. VI, pp. 251-259, 1904.

WHEELER finds that under natural conditions the food of *Leptogenys elongata* consists very largely, if not exclusively, of the isopods *Oniscus* and *Armadillidium*. This is the only ant known to show so marked a preference for crustacean food; the other members of the same genus appear to feed for the most part upon termites.

The males of *L. elongata* are winged, but the females are apterous, in appearance much resembling the workers. How the fertilization of the females takes place is thus an interesting question. Of course a nuptial flight is precluded by the wingless condition of the females, and WHEELER considers it improbable that the males of one nest find their way into other nests and so fertilize the females there. If the females are fertilized by the males of the same colony, the author points out that this would be a most flagrant case of inbreeding, so it seems reasonable to suppose that the females issue from the nest at night as pedestrians and in this way meet the males of other nests, as the latter also go forth at night. The males are said to be "highly heliotactic."

L. J. COLE.

Marshall, Wm. S. The Marching of the Larva of the Maia Moth, *Hemileuca maia*. *Biol. Bull.*, Vol. VI, pp. 260-265, 1904.

A number of rather desultory experiments were made upon the marching columns of the recently hatched caterpillars of *Hemileuca maia*. It was found that when the leading caterpillar of a line was removed the procession was stopped and the larvæ gathered into a bunch. In nine out of twenty-one experiments the original leader when returned again took the lead and the line followed; in the other eleven cases a new leader took the place of the one removed. No general conclusions are drawn.

L. J. COLE.

Adams, Chas. C. The Migration Route of Kirtland's Warbler. *Bulletin Michigan Ornith. Club*, Vol. V, pp. 14-21, 1904.

A study of the migration routes of this warbler, with maps and suggestions of conditions which influence migration.

R. M. Y.

- Ritter, Wm. E. and Davis, B. M.** Studies on the Ecology, Morphology and Speciology of the Young of Some Enteropneusta of Western North America. *University of California Publications—Zoology.*, Vol. 1, pp. 171-210, Pls. 17-20, 1901.

The ecological portion of this report is concerned chiefly with the movements of *tornaria*, and the conditions which determine them. The organisms swim upward in the water because of a difference in specific gravity of the two ends. There is no satisfactory evidence of the importance of temperature or light in the orientation of the organisms. The stroke of the cilia is invariable in direction. R. M. Y.

- Ritter, Wm. E.** Further Notes on the Habits of *Autodax Lugubris*. *American Naturalist*, Vol. XXXVII, pp. 883-886, 1903.

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R. M. Y.

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WALLACE CRAIG.

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This paper contains several interesting facts concerning the natural history of the insect.

R. M. Y.

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RETROGRADE DEGENERATION IN THE CORPUS CALLOSUM OF THE WHITE RAT.

By S. WALTER RANSON.

*(From the Neurological Laboratory of the University of Chicago and the Anatomical
Laboratory of St. Louis University.)*

With Plate VII

SUMMARY OF THE LITERATURE.

It was maintained by WALLER (6) and those who immediately followed him that the end of the nerve fiber attached to the cell body did not degenerate as the result of section of the fiber. Evidence has, however, been steadily accumulating to show that this view is incorrect. The facts bearing on this point have been brought together by FLEMING (1), KLIPPEL and DURANTE (2), and VAN GEHUCHTEN (4). These authors review the literature in great detail; but only the briefest summary will be given here, and this will be based chiefly on the excellent review by VAN GEHUCHTEN.

The first observations not in harmony with the law of WALLER were made upon cases of long standing amputation. Atrophy of the ventral and dorsal root fibers and of the part of the spinal cord associated with the nerves of the amputated limb has been found in these cases. (DICKINSON, '68, VULPIAN, '68, HAYEM and GILBERT, '84, MARINESCO, '92, and others). Experimental amputations of the limbs of animals, involving section of the peripheral nerves, have confirmed these observations (VULPIAN, '69 and HAYEM, '73), and shown the presence of fibers with fragmented myelin in the central ends of the cut nerves. Degenerating fibers were also found in the ventral and dorsal nerve roots and in the dorsal fasciculi of the cord. (DARK-SCHIEWITSCH, '92 and MOSCHAEW, '93).

The second group of observations opposed to the statement formulated by WALLER has been derived from experiments intended to locate the nuclei of origin of the motor nerves. The tearing out of motor nerves is followed by atrophy or disappearance of their intramedullary roots and nuclei of origin. (Literature summarized by FOREL, '87.) A true degeneration of the central ends of these fibers can be demonstrated by the method of MARCHI (BREGMANN, '92, DARKSCHEWITSCH, '92).

In the central nervous system a retrograde or cellulipetal degeneration has been observed in seven localities. A descending degeneration has been seen in the optic radiation after excision of its terminal ramifications in the occipital cortex (VON MONAKOW, '84, MOELI, '93) and in the medial lemniscus after injury to the central gyri (VON MONAKOW, '85, GREIWE, '94, KLIPPEL and DURANTE, '95). The retrograde degeneration in these tracts differs in some cases histologically from WALLERIAN degeneration, the axis cylinder remaining intact while the myelin sheath disappears, although in most cases it resembles true secondary degeneration very closely. Often this cellulipetal degeneration is very extensive, involving the majority of the fibers of the tract. For these reasons, the downward degeneration in the optic radiation and in the lemniscus cannot be adduced as evidence for a double pathway. Similar observations have been made on the pyramidal tract, which in certain cases has degenerated cephalad after a transverse lesion of the spinal cord (WILLAMSON, '93, RAYMOND, '94).

VAN GEHUCHTEN has shown that degeneration of the proximal part of injured nerve fibers may occur in the middle cerebellar peduncle, in the fibers passing from the nucleus ruber to the lateral fasciculus of the spinal cord, in the fibers passing from the nucleus of DEITERS to the anterior fasciculus of the cord, and in those from the cells of the formatio reticularis of the pons and medulla to the antero-lateral fasciculus of the cord. That retrograde degeneration occurs in these tracts and not merely the WALLERIAN degeneration of a second pathway, is supported by the facts that the changes in question do not ap-

pear until fifteen days after WALLERIAN degeneration has begun and that the cells of origin of these tracts disappear.

OBSERVATIONS ON THE WHITE RAT.

Introduction and Summary.

In a previous paper the writer (3) called attention to the complete degeneration of the splenium of the corpus callosum in a young rat after deep incision of the occipital lobe, and reference was made to a similar observation by VON GUDDEN (5). If this degeneration had occurred according to WALLER's law, about half the normal number of fibers should have been present on each side of the lesion. But in this case all the fibers had disappeared. This means that the fibers underwent serious alterations in both directions from the point of injury. This observation taken by itself only shows the absence of the myelin sheath in the proximal portion of the injured fiber, as no stains were used which would demonstrate the presence or absence of naked axis cylinders. Since there were no medullated fibers in the corpus callosum at the time of the operation the absence of myelin might be interpreted as due to an arrest of development. But further observations made on older rats have shown that a true degeneration closely resembling the WALLERIAN type may occur in the proximal portions of severed fibers.

The chief difference between the changes in the proximal and the distal portions is that the latter pass more rapidly through the stages of fragmentation, solution and absorption, these changes affecting the whole extent of the severed portion at the same time; while in the proximal portions the changes occur somewhat later and may involve only the part of the fiber nearest the point of injury. Thus forty-five days after a wound is made in the medullated corpus callosum of young rats (21 to 70 days of age) the ordinary WALLERIAN degeneration has run its full course and the resulting debris is entirely absorbed. But at this time fragmentation of myelin may be distinctly seen in the proximal portions of the severed fibers, affecting especially the part in the vicinity of the lesion.

Operative Technique.

Through the occipital portion of the corpus callosum in rats of various ages (0.5, 3, 7, 21, 30, 40, 60, 70 days old), an incision was made in the left cerebral hemisphere about one millimeter to the left of the great longitudinal sinus and two millimeters frontal to the lateral sinus, in such a way that a wound one and a half millimeters long and two or three millimeters deep was made in the posterior part of the occipital lobe, parallel to the midplane. The animals were killed forty-five days after the operation. In each case serial frontal sections through the left occipital lobe were prepared according to the PAL-WEIGERT technique.

Results.

In so simple an operation asepsis is not difficult to obtain. The wounds were covered with collodion and remained well protected until healing had taken place. The animals recovered rapidly and after twenty-four hours appeared to be perfectly normal. During the entire subsequent period they were in excellent physical condition, and equaled in weight the rats of the same age in the laboratory. In only one case did the post-mortem examination show any trace of inflammatory reaction. In this rat slight adhesions were present between the dura and the brain scar, but these produced no appreciable effect on the results.

The mildest form of the cellulipetal degeneration is found in the brain of the oldest rat (seventy days old at the time of operation). Except for the comparatively narrow band of scar tissue, there is no area in which complete degeneration of all the fibers has taken place. Portions of many fibers must have been cut off from their cells of origin, and these portions have no doubt undergone complete WALLERIAN degeneration, although the debris resulting from their disintegration has been entirely absorbed. Thus on each side of the cicatrix there is brain tissue which at first sight appears normal. But on closer examination many of the fibers in the immediate vicinity of the scar are found to differ from the normal in that they have an

irregular contour, being very much constricted at certain points and swollen into beads at others. Most of these fibers stain well by the PAL-WEIGERT method. Their myelin has not been gathered into droplets nor been to any appreciable extent absorbed. These beaded fibers are not to be found more than two millimeters on either side of the line of incision since the cellulipetal degeneration had extended only a short distance along the fiber.

In a rat ten days younger (sixty days old at the time of operation) there are considerable areas of degeneration in the substantia alba. Figure 1, "a" shows a Y-shaped area of faint staining extending medialward from the scar. There is also a slender unstained band extending lateralward. In these areas the cellulipetal degeneration has progressed somewhat farther than in the case previously described. Near the line of incision all the myelin has been absorbed, leaving only the faintest outline of the fibers visible. Figure 2 is a drawing of a small portion of the degenerated area represented at "a" in Figure 1. In addition to the beaded fibers described in the previous case there are many that are faintly stained, some of which contain minute droplets of myelin. There are also many large faintly stained drops of myelin which do not appear to be connected with fibers.

In the rat which was thirty days old at the time of the operation, the process of cellulipetal degeneration has increased in intensity and extended farther along the fibers. Figure 3, "a", shows a comparatively wide band in the substantia alba faintly stained because of the disappearance of most of the fibers. Near the line of incision this disappearance of fibers is complete; only a few scattered drops of myelin are visible. Farther lateralward (Fig. 4) are fibers in the process of disintegration, some swollen and beaded, other faintly and irregularly stained. Still farther lateralward these give place to normally stained, smoothly contoured fibers.

Changes similar to those described above were found in the brain of a rat operated on when twenty-one days old; but here fibers were found degenerating at a much greater dis-

tance from the point of injury. Fig. 5 shows that most of these fibers are in the last stages of degeneration. They are very irregular in shape, and their outlines are only faintly visible. They stain faintly except in a few places, where there still remain minute globules of myelin. They are broken up into short segments, so that no fiber can be followed for any considerable distance. A few droplets of free myelin are still unabsorbed.

In order to interpret these results it is necessary to bear in mind the condition of medullation in the corpus callosum of the young rat. WATSON (7) has shown that medullation in this region begins about the fourteenth day. Thus, fibers cut in the operation performed on the twenty-first day are both structurally and functionally very immature; and the rapidity with which they degenerate is, no doubt, closely related to this condition. By the seventieth day the neurones have attained a greater degree of stability, which shows itself in the much more limited retrograde degeneration. When the operation was made on or before the seventh day of age no medullated fibers were cut, because there were none present. This would account for the fact that in examining the preparations of these brains no fibers with disintegrating myelin sheaths were found. There are, however, areas which are almost devoid of fibers, although they exhibit a few that are slender, normally contoured and well stained. On the basis of the earlier experiments (3) these are to be explained as having developed since the injury. Complete degeneration is best seen in the corpus callosum of the rat operated on when twelve hours old, which has been figured in the *Journal of Comparative Neurology*, Vol. XIII, Plate VII, Figures 4 and 7. Much the same condition is seen in the corpus callosum of the next older rat (3 days); but in this and the one operated on at the seventh day the wound is situated so far posteriorly, that the picture is complicated by the presence of fibers curving backward into the occipital lobe. These fibers, coming from in front and passing backward and outward, cross the zone which would otherwise be free from fibers.

As has been already stated, this paucity of medullated fibers in the corpus callosum, so evident in the youngest rat,

might be interpreted as due to a failure of development of the medullary sheaths about the central portions of the severed axones; or it might be due to the complete disappearance of these axones. But when one takes into consideration the retrograde degeneration seen in these fibers in the older rats, there can be little doubt that the degeneration is of the same nature in these younger animals and that the entire neurone has undergone disintegration.

If it is remembered that all these animals were allowed to live for one month and a half after the operation, it will be seen from what has been said that the intensity of the cellulipetal degeneration exhibited in any portion of the section depends upon two variables, the age of the animal and the distance between the point of observation and the point of injury. In the oldest rat the process was confined to a small portion of the fiber near the lesion. As we pass down the series from the oldest to the youngest animal, the degeneration increases in intensity in the vicinity of the lesion, and extends to a greater distance from the point of injury. The complete degeneration of the fibers in the older rats takes place only in the immediate vicinity of the lesion, but in the youngest animal the fibers degenerate completely throughout their entire length.

There are several respects in which the changes here described differ from the WALLERIAN degeneration. In typical secondary degeneration the myelin begins to liquify at the sixth day and is largely absorbed before the twentieth. But in the milder cases of the degeneration here described there are many fibers remaining after forty-five days which differ from the normal only in the presence of a few beadlike swellings, the rest of the fiber remaining normal in contour and staining properties. And in these milder cases there are no fibers present in which the myelin has undergone liquefaction. It is evident that the secondary degeneration, which must have occurred in the portions of the fibers separated from their cell bodies, has run its full course and the resulting debris been entirely absorbed. Otherwise we could not account for the complete absence in some of these cases of fibers in the last stages of degeneration.

The degeneration which is seen beginning in certain fibers 45 days after the lesion is, therefore, a process commencing after the ordinary secondary degeneration is complete. Another feature which distinguishes retrograde degeneration from secondary degeneration is the fact that the latter occurs simultaneously throughout the entire length of the severed part, while the former may involve only a small part of a fiber in the immediate vicinity of the lesion.

A word may be said regarding the nature and cause of this degeneration of the proximal part of injured fibers. VAN GEHUCHTEN (4) has shown that associated with these changes in the fiber leading to its disintegration, there is a chromatolysis of the cells of origin resulting, in certain cases, in their complete destruction. In those neurones in which this occurs he believes that the degeneration of the fiber follows on the death of the cell and proceeds down the fiber toward its terminals. For this reason, he objects to the use of the term "retrograde" in designating this type of degeneration, because it indicates that the degeneration begins at the point of injury and proceeds toward the cell body.

It is, however, quite conceivable that the evidence of this disintegration of the neurone should be found first in the portion of the neurone farthest separated from the nucleus, namely at the tip of the fiber near the lesion. As a matter of fact many of the preparations upon which this paper is based show a degeneration in the end near the lesion while the rest of the fiber appears normal. In some cases beginning near the lesion and tracing the fiber toward the cell of origin one may see all the stages of degeneration; at first the fiber stains faintly because of the absorption of its myelin, then it is found to be well stained but of irregular contour and finally it takes on a perfectly normal appearance. It seems clear, therefore, that in this case at least the process is a true retrograde or cellulipetal degeneration.

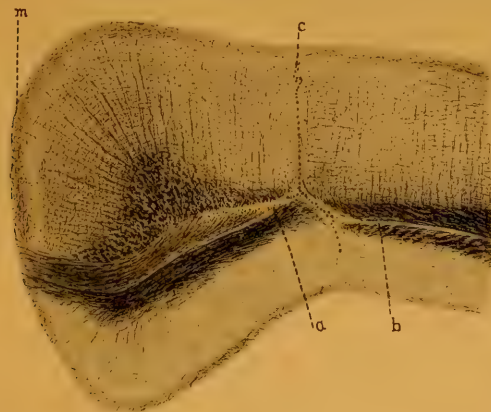


Fig. 1



Fig. 3

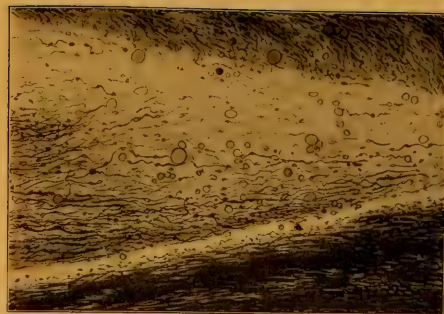


Fig. 2
(Point "a" figure 1 enlarged)

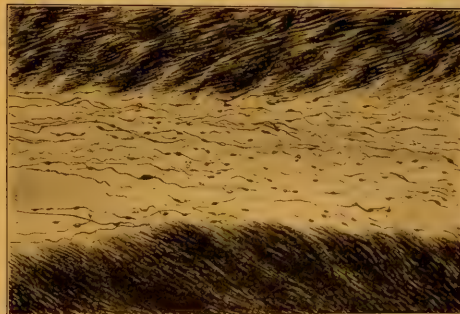


Fig. 4
(Point "a" figure 3 enlarged)



Fig. 5

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DESCRIPTION OF PLATE VII.

The drawings, made by Mr. A. B. STREEDAIN, represent retrograde degeneration in the corpus callosum of white rats, killed forty-five days after the making of an incision in the occipital lobe. They were made from PAL-WEIGERT preparations of frontal sections through the occipital lobe.

Figure 1 is from a rat operated on when sixty days old.

a and *b*, degenerating areas.

c, line of incision.

m, medial surface of the hemisphere.

Figure 2 is from the same preparation as the former drawing. It represents the appearance under the oil immersion lens of a small area designated by "*a*," *Figure 1*.

Figure 3 is from a rat operated on when thirty days old. The lettering is the same as in *Figure 1*.

Figure 4 is from the same preparation as *Figure 3*. It represents a small area at "*a*" seen under the oil immersion lens.

Figure 5 was drawn with the aid of the oil immersion from the degenerating corpus callosum of a rat operated on when 21 days old.

THE EARLY HISTORY OF THE OLFATORY NERVE IN SWINE.¹

By EDGAR A. BEDFORD, S. M.

With fourteen figures in the text.

From 1862, the time of the first examination, from the standpoint of modern science, of the structure of the olfactory nerve by MAX SCHULTZE,² up to the present time, various observations have been made upon the structure and development of the olfactory nerve.

Some of the views held by older investigators have been superseded. There has been a growing tendency to depart from the earlier belief, that the olfactory nerve arises from the brain, to a belief that it originates in the periphery. This view is in harmony with the teachings of HIS that all sensory fibers originate in the periphery. However, since this nerve differs, in some respects, in histological structure from other nerves, too much dependence must not be placed upon analogies drawn from the development of other nerves. Our views concerning the development of this nerve, therefore, must be based upon the observations regarding its individual development.

The anatomists of the middle of the 19th century looked upon the olfactory nerve as part of the brain, confusing it with the olfactory tractus and bulb. Gradually this view began to be controverted and evidence was brought to show that both the optic and olfactory are true cranial nerves, although very

¹ Contribution from the Zoological Laboratory of Northwestern University, WILLIAM A. LOCY Director.

² MAX SCHULTZE. Untersuchungen über den Bau der Nasenschleimhaut. *Abhandlungen der Naturforschenden Gesellschaft zu Halle*, Bd. VII, 1862.

much modified. Up to very recent time, there has been confusion, even among writers of the highest merit.

HERTWIG,¹ as late as 1892, says: "Finally in treating of the development of the cerebrum, there is still to be considered an appendage of it, the olfactory nerve. This part as well as the optic nerve is distinguished from the peripheral nerves by its entire development and must be considered as a specially modified portion of the cerebral vesicle. The older designation of nerve, therefore, is now more frequently replaced by the more appropriate name of olfactory lobe." HERTWIG then goes on to describe the development of the lobe of man, completely ignoring the development of the fibers which form the real olfactory nerve. The true condition is made clear by EDINGER.² "From the epithelium of the nasal mucous membrane long terminal fibrillae run backward. They are called fila olfactoria and pass through the cribiform plate into the cranial cavity. . . . The fila olfactoria pass to an anteriorly directed evagination of the fore-brain vesicle. This evagination forms on the base of the brain a more or less elongated tube which, in most animals, remains hollow, tractus and bulbus olfactorius." Further he says that the tractus, which connects the bulbus with the remaining portion of the brain, in some animals, might easily be taken for the olfactory nerve, which, however, terminates at the olfactory bulbus.

LEE,³ LOCY⁴ and others have directed attention to the true relation of the fila olfactoria and the tractus. It is with the development of these fila olfactoria that this paper is concerned.

¹ OSCAR HERTWIG. Text-Book of the Embryology of Man and Mammals. Translation by EDWARD L. MARK, pp. 448-449.

² EDINGER. HALL'S Translation, p. 146.

³ LEE. Zur Kenntniss des Olfactorius, *Berichte Naturf. Gesellsch. Freiburg*, Bd. VII, 1893.

⁴ WM. A. LOCY. New Facts Regarding the Development of the Olfactory Nerve, *Anat. Anz.*, XVI, pp. 273-290.

Résumé of Literature.

One of the earliest investigators to consider the development of the olfactory nerve was MILNES MARSHALL¹ (1878-1879). He describes the first appearance of the olfactory nerve in the chick, as "a small outgrowth of spherical or slightly fusiform cells, arising on either side from near the top of the forebrain." "This small process," MARSHALL claims, "may be traced for a short distance in successive sections running downward and slightly outward, lying close to, but perfectly independent of the external epiblast. At this period there is hardly a perceptible thickening of the epiblast at the spot where the olfactory pit will shortly afterwards appear. It is toward this point the growth is directed."

It is evident from reading MARSHALL'S papers that he began his work with the preconceived idea that the olfactory nerve arises from a continuation forward of the neural ridge. His observations are all made from that standpoint. It will be seen later how, by failing to observe the very first stages in the formation of the olfactory nerve, and by making a slight error in the observation of other stages, he might be led to believe that he had evidence of the origin of the olfactory nerve from the brain. In order to further support his attempt to homologize the olfactory with other nerves, he attempts to homologize the nasal pits with a pair of gill clefts. MINOT, in his textbook of embryology, points out that "MARSHALL failed to attribute weight to the fact that the gill clefts are primarily evaginations of the endoderm while the nasal pits are invaginations of the ectoderm."

BALFOUR² who preceded MARSHALL in the examination of the olfactory nerve came to the conclusion that in the elasmobranchs it originates from the peripheral end of each olfactory lobe. Thus, BALFOUR, as MARSHALL, believes in a cranial origin for the olfactory nerve. The only point in which he materially differs from MARSHALL is in the fact that he believes that the nerve arises from the olfactory lobe, while MARSHALL believes that, in both the elasmobranchs and the chick, it arises before an olfactory lobe has been formed.

¹ MILNES MARSHALL. The Development of the Cranial Nerves in the Chick, *Quart. Journ. Micros. Sc.*, Vol. XVIII, 1878.

Morphology of the Vertebrate Olfactory Organ, *Quart. Journ. Micros. Sc.*, Vol. XIX, 1879.

² FRANCIS BALFOUR. *Journal of Anatomy and Physiology*, Vol. XI, 1878.

A. VON KÖLLIKER¹ is another able investigator who claimed a central origin for the olfactory nerve. His observations were made upon mammals.

In 1890, however, he completely changed front and claimed a peripheral origin for the nerve in both the chick and mammals. In mammals he found (in the material at his disposal) the olfactory nerve always firmly attached to the epithelium of the olfactory pit. He found, however, no stage in which the olfactory nerve was connected with the olfactory pit without also being connected with the brain wall, yet he considers it evident that the olfactory nerve arises in the olfactory epithelium and grows toward the brain. KÖLLIKER believes that the nuclei in the adult nerve belong to the nerve fibers themselves and that each fiber contains several nuclei. "Each fiber corresponds to a complex of nerve cells." The presence of mitoses within the anlage is regarded as evidence that the cells lengthen and form fine fibers, while the nuclei divide several times.

BEARD,² in his *System of Branchial Sense Organs and their Associated Ganglia in Ichthyopsida*, gives still another explanation of the origin of the olfactory nerve. He claims that the anlage of that nerve is made up of cells arising from both the brain and the nasal epithelium. A cell-mass grows from the forebrain, cells from the epithelium become connected with this and thus the ganglion is fully formed. BEARD's observations were made upon the Torpedo. His general scheme of nerves is based upon conditions found in some of the more posterior nerves. He has found that in the selachians, the nerves that supply the gill arches are formed through the union of the two anlages, one arising from the brain and one arising as a thickening of the overlying region of the integument. BEARD, in support of his view, attempts to homologize the nasal epithelium with a branchial sense organ.

CHIARUGI³ agrees very closely with BEARD. He concludes that,

¹ A. VON KÖLLIKER. *Entwicklungsgeschichte*, 1879.

Ueber die erste Entwicklung der Nervi olfactorii, *Verhandl. d. physikalisch med. Ges. zu Würzburg*, Sitz. von 6 Juli, 1890.

² J. BEARD. *The System of Branchial Sense Organs and their Associated Ganglia in Ichthyopsida*, *Quart. Journ. Micros. Sc.*, Nov., 1885.

³ CHIARUGI. Observations sur les premieres phases du developpement des nerfs encephaliques chez les mammiferes, et, en particulier, sur la formation du nerf olfactif, *Archiv. Italiennes de Biologie*, XV, 1891.

in the guinea pig, the cellular anlage of the olfactory nerve is made up of cells arising both from the brain and epithelium of the olfactory pit. The evidence, however, which he presents is not very conclusive. CHIARUGI found a fibrillar stage following a purely cellular stage. He believes that more than one fiber may arise from one cell.

HIS¹ was the first to affirm that the olfactory nerve arises exclusively from the periphery. Since his views have exerted such a great influence upon those held at present concerning the origin of the olfactory nerve, it will be well to examine his work in detail.

He finds, first, in a four and one-half week old human embryo, a mass of cells lying near the olfactory plate, which he calls a ganglion, having apparently no connection with the brain. But even in earlier stages he finds in the olfactory plate, as in the medullary plate of the same period, two kinds of cells, one of which later becomes neuroblasts with fibrillar processes, while the other contributes to the formation of the supporting elements. HIS states that the cells which will form the neuroblasts, wander out of the olfactory epithelium, to form the ganglion. It is the processes of these cells which form the fibers of the olfactory nerve. The cells are bipolar, one process passing to the olfactory epithelium, the other passing toward the brain. Later the cell bodies pass toward the bulbus and are found in the cap-like covering of the bulbus. He believes that the nuclei lying in the course of the adult nerve do not belong to the fibers, but to the cellular nerve sheath.

DISSE² applied GOLGI's method to the study of the various stages in the development of the olfactory nerve in the chick. He agrees with HIS that the olfactory fibers arise from the neuroblasts that origi-

¹ W. HIS. Ueber die Entwicklung der Riechlappens und des Reichganglions und über diejenige der verlängerten Marks, *Verhandl. d. Anat. Gesellschaft*, 1889.

Die Formentwicklung des menschlichen Vorderhirns, *Abhandl. d. math.-phys. Klasse der Kgl. Sächs. Gesellschaft. d. Wissenschaften*, Bd. XV, 1890.

² DISSE. Ueber die Erste Entwicklung des Riechnerven. *Sitzungsberichte der Gesellschaft zu Beförderung der gesamten Naturwissenschaften in Marburg*, No. 7, October, 1896.

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On the Early Development of the Olfactory Nerve. *Proceedings of the Anatomical Society of Great Britain and Ireland*, published in the *Journal of Anatomy and Physiology*, 1901.

nate within the olfactory epithelium. DISSE, however, believes that the majority of the neuroblasts never leave their position within the olfactory epithelium. A very few do pass into the mesoderm separating the olfactory epithelium from the brain and there undergo their transformation into bipolar ganglion cells. He also believes, as does HIS, that the cellular anlage of the olfactory nerve, which has been seen by various observers, arises from cells that migrate from the olfactory epithelium, but these cells, according to DISSE, instead of becoming neuroblasts are destined to form the cellular nerve sheath. Thus he believes that the cell mass, which by other investigators has been considered to be the anlage of the olfactory nerve, is of very slight importance in the formation of that nerve. He failed to obtain satisfactory results from the use of the GOLGI method in the study of mammalian embryos.

Even if DISSE's work be accepted as representing the true condition in the chick, it does not necessarily follow that the course of the development of the olfactory nerve is precisely the same for mammals.

The observations of HIS, VON KÜLLIKER and CHIARUGI, only, are based upon the study of mammalian embryos. In BEARD, VON KÜLLIKER, CHIARUGI, HIS and DISSE, whose work has been done since 1884, we have five investigators, no two of whom are in entire agreement as to the origin of the olfactory nerve. CHIARUGI's conclusions, based upon the observation of mammalian embryos, differ very essentially from those arrived at by HIS and VON KÜLLIKER in the study of animals of the same class. HIS and VON KÜLLIKER in turn do not agree as to the relation of the cells to the fibers of the nerve and neither of these investigators employed the GOLGI method by the use of which DISSE reached in the chick very different conclusions as to the position of the neuroblasts from which the fibers arise.

Scope of This Paper.

It is evident that there is need of more observations regarding the origin of the olfactory nerve. It is especially desirable to ascertain whether the conclusions arrived at by DISSE for the chick can be extended to mammals.

Since the conclusions of the different investigators vary, the following pertinent questions have not, as yet, for mammals been conclusively answered.

1. When and where do the first indications of the olfactory nerve appear?

2. If in the olfactory epithelium, is there also any indication of a portion of the anlage arising from the brain?

3. Do the cells of the so-called anlage become ganglion cells.

4. If these are ganglion cells, what is their location in the adult nerve?

5. If these cells are not ganglion cells, what is their fate and where are the true ganglion cells located?

The writer has undertaken to trace the history of the olfactory nerve in swine, from its first indication onward to the sub-adult stage, and believes that in addition to giving a general history of its development, he is able to throw some light on all the above questions. But the fate of some of the cells of the so-called primitive anlage remains unsettled.

The work was undertaken at the suggestion of Professor WILLIAM A. LOCY of the Northwestern University, whom the writer has to thank for much valuable direction.

Personal Observations.

Methods.—Perfectly fresh material for fixation was obtained by plunging the embryos, removed from uteri of recently killed swine directly into the fixing fluid. At the time of their removal from the uteri, the hearts of the embryos were still normally beating.

The most satisfactory results were obtained from material fixed in VOM RATH'S picro-platin-osmic mixture and stained with iron haematoxylin. Embryos fixed in corrosive-acetic and stained with either DELAFIELD'S haematoxylin or iron haematoxylin gave good results.

For GOLGI preparations the rapid method was used. Some very good results were obtained with GOLGI from material that had been preserved in ten percent formalin for a week or more.

Formation of the Olfactory Pit.—Soon after the closure of the neural groove, a thickening, caused by the cells of the ectoderm becoming elongated, appears well forward upon each side, of the head region. This is the olfactory plate.

At this time the greatest thickness of the olfactory plate

is .075 millimeter. From the region of greatest thickness, it gradually thins out in every direction until the ordinary thickness of the general epithelium is reached, which is .001 millimeter. Such a condition of the epithelium is found in a swine embryo of five millimeters length. Even at this time may be seen a slight indentation in the olfactory plate. In older embryos this indentation becomes deeper. This is due to the more rapid growth of the margins of the plate.

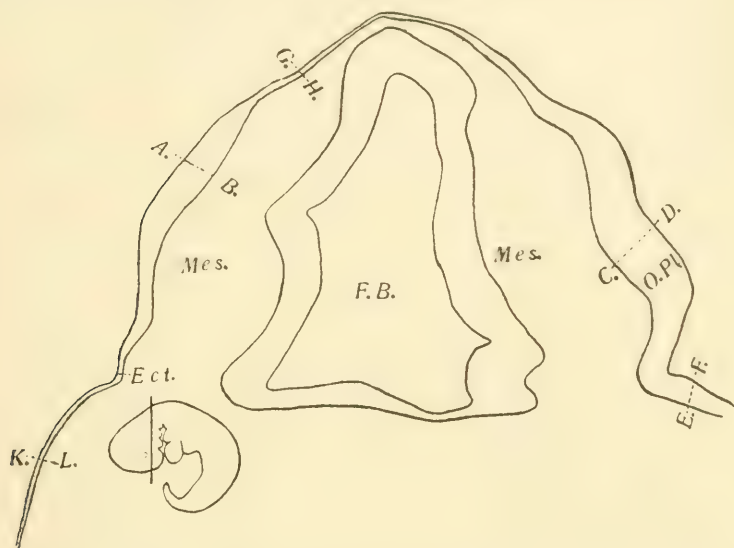


Fig. 1. Section through the head of a swine embryo, 5 mm. long, in the plane indicated in the small figure, showing the thickening of the epithelium at future location of olfactory pit. *A-B* .05 mm., *C-D* .075 mm., *E-F* .025 mm., *G-H* .001 mm., *K-L* .0012 mm., *F. B.*, forebrain, *Mes.*, mesoderm, *Ect.*, ectoderm, *O. Pl.*, olfactory plate.

As the deepening increases the pit comes to occupy a more ventral position and to lie relatively nearer the mid-line. In an embryo in which there is the earliest appearance of a pit, the distance between the two pits is practically the entire width of the head, while in an embryo of about eleven millimeters in length, the distance between the two pits constitutes only fifty-five percent of the entire width of the head.

In a young embryo in which the pit is just beginning to form, the axis of the lumen is directed outward at a right angle

to the lateral aspects of the head. As the embryo becomes older the axis of the lumen gradually shifts until it is directed ventrally, having passed through an angle of nearly 90 degrees.

Up to the time of the first appearance of the nerve the pit has the form of a simple invagination. No folds as yet have appeared in its walls. Thus a well-formed pit has developed before there is any indication of the olfactory nerve.

Differentiation of the Cells of the Olfactory Epithelium.— In embryos possessing an olfactory plate in which only a very slight indication of an invagination appears, two kinds of cells may be seen in the epithelium; first, the ordinary prismatic cells; second, large cells almost spherical in shape, whose cytoplasm is not readily stained. The latter are usually located in groups of three or four. In embryos of this stage of development they are always situated near the external margin of the epithelium. In an embryo of six millimeters, in which the dif-

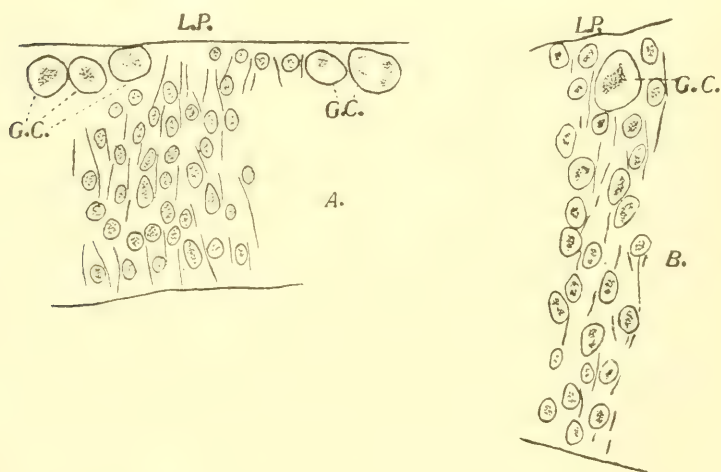


Fig. 2. Sections of olfactory epithelium showing germinating cells, *G. C.*, located near lumen of the nasal pit; *L. P.*, Lumen of Pit. Iron haematoxylin. A, from an embryo 9 millimeters in length; B, from an embryo 6 millimeters in length. $\times 533$.

ferentiation of the cells was first observed, a number of these cells show different stages of karyokinetic division. The nuclei

of these cells are more nearly spherical than the nuclei of the prismatic cells, the nuclei of the latter being usually elliptical, their long axes corresponding with the long axes of the cells. The nuclei of the rounded cells are not provided with a nuclear membrane and present a ragged outline. As has been often suggested, they are probably mitotic cells.

Development of Neuroblasts.—In slightly older embryos, in addition to the spherical cells, cells of a slightly different shape are present, which, from their size, appearance and location, evidently belong to the same class of cells as the spherical cells described. They are pear-shaped with the pointed end directed away from the outer edge of the epithelium, toward that margin bordering the mesoderm.

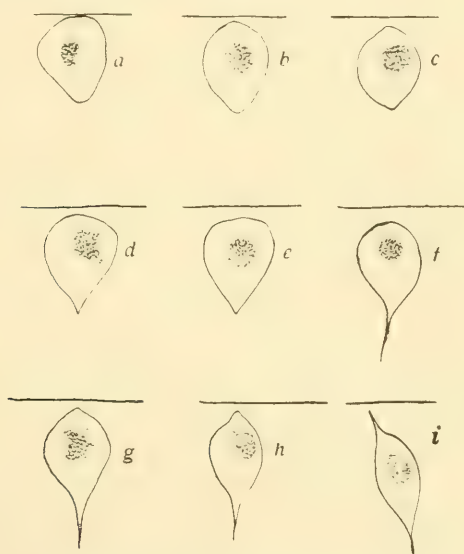


Fig. 3. Various stages in the development of neuroblasts observed in the olfactory epithelium of a swine embryo 7 millimeters in length. The line above each figure represents boundary between epithelium and the lumen of the nasal pit. $\times 800$; iron haematoxylin.

In a number of cases this pointed end passes into a fine fiber extending toward the mesodermal margin of the epithelium. In the majority of cases, the peripheral end is very slightly pointed, while in other cells a well developed, con-

siderably elongated, conical elevation is present on the peripheral end of the cell. In these cases the cell body is removed somewhat from the outer margin of the epithelium and the central fiber is well developed. All intermediate stages, from a spherical cell through a pear-shaped cell, from the apex of which a fiber passes toward the central border of the epithelium, to a

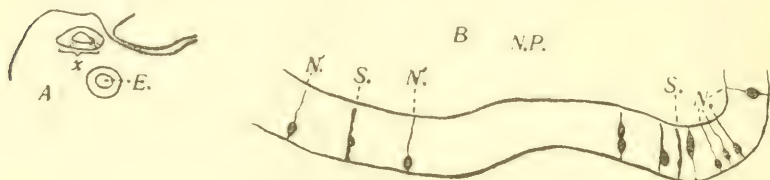


Fig. 4. *A*, Longitudinal section of a swine embryo, 13 millimeters in length, through the nasal pit. *E*, eye. $\times 8$.

B, Portion of olfactory epithelium of *A* (*x*) showing developing nerve cells (*N*) and supporting cells (*S*). *N. P.*, nasal pit. $\times 93\frac{1}{3}$. GOLGI preparation. bipolar cell, are found (Fig. 3). These cells conform very well to developing neuroblasts described by HIS, and called by him germinating cells. Not until some time after this is there any structure present between the epithelium of the olfactory pit and the brain wall, which might be considered to be the anlage of the olfactory nerve.



Fig. 5. Section of olfactory epithelium of a swine embryo, 17 millimeters in length, showing developing nerve cells (*N*). GOLGI preparation. $\times 93\frac{1}{3}$.

By the use of the GOLGI method, both the developing nerve cells and supporting epithelial cells are impregnated. The latter are quite irregular in outline, while each of the former has an enlarged cell body which tapers at either the peripheral or the central pole of the cell or at both poles into a slender unbranched process. In GOLGI preparations, the de-

veloping nerve cells are seen to be located at different levels within the epithelium. *B* and *B'*, Fig. 6, represent neuroblasts whose cell bodies are located upon the margin of the epithelium bordering the lumen of the nasal pit. *N*, Figs. 4,

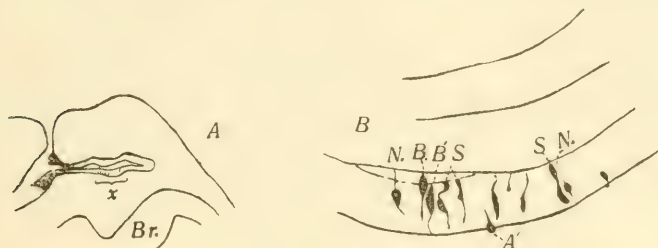


Fig. 6. *A*, Sagittal section through head of an embryo 17 millimeters in length. *Br.*, wall of forebrain. $\times 8$. *B*, Portion of olfactory epithelium ($\times 93\frac{1}{3}$) indicated in *A'* by brace (*x*), showing developing nerve cells (*N*) and supporting cells (*S*). *A'* represents a neuroblast that has migrated partially into the mesoderm. GOLGI preparation.



Fig. 7. Developing nerve cells from the olfactory epithelium of a 15 mm. swine embryo, one with central process directed into an elevation of the epithelium. *N. P.*, Nasal pit. $\times 140$. GOLGI preparation.

5 and 6 represents developing nerve cells whose cell bodies are considerably removed from the margin of the epithelium bordering the lumen of the pit. *N'*, Figs. 4 and 5 represents nerve cells whose cell bodies are located nearer the mesodermal margin of the epithelium. *A'* of Fig. 6 represents a developing nerve cell that is partially outside of the olfactory epithelium, lying partially within the mesoderm. The GOLGI preparations were made from embryos of thirteen millimeters and upward in length.

Beginning of Outgrowth from the Nasal Epithelium toward the Brain Wall.—In embryos from nine to twelve millimeters in length, the median wall of the olfactory pit becomes relatively thicker than the lateral wall. At the same time, the

margin of that portion of the wall bordering the mesoderm shows a slight waviness. Earlier stages show no indication of such a condition, nor do other portions of the olfactory wall in the same embryos (Figs. 8 and 9).

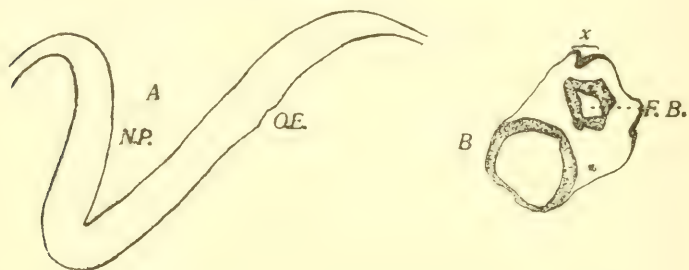


Fig. 8. *A*, Section of olfactory epithelium of a swine embryo 9 millimeters in length. *N. P.*, nasal pit; *O. E.*, elevations of the olfactory epithelium. $\times 93\frac{1}{3}$. *B*, Section through head, a portion of which (*x*) is represented by *A*. *F. B.*, forebrain. $\times 7\frac{1}{3}$.

This waviness on the mesodermal margin of the epithelium develops into distinct elevations. These elevations appear to be caused by the pushing toward the mesoderm of the cells of the epithelium. Histologically, these cells seem to be, for the most part, the ordinary epithelial cells. In a few instances, they resemble the germinating cells found near the outer margin of the epithelium.

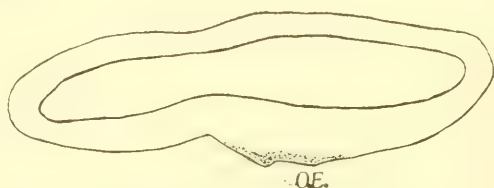


Fig. 9. Section through the walls of the olfactory pit of a 12 mm. embryo, showing at *O. E.* the elevations mentioned in the text.

The section shows also the variations in thickness of the epithelial walls. $\times 93\frac{1}{3}$.

In earlier stages the nuclei of those cells nearest the inner margin are arranged in a row at a definite distance (.00875 mm.) from the inner border. See Fig. 10, *A*. This arrangement is also to be noted in the later stages in those portions of the epithelium away from the elevations mentioned above.

This, however, is not found to be the case in those thickened portions of the epithelium of the same section where the waviness of the mesodermal edge and the elevations occur. By examination of Fig. 10, *B* it will be observed that some nuclei have passed beyond the general line of nuclei and have come to occupy a position much nearer the mesoderm. Fig. 10, *C* shows an outpitting of the epithelium in which the nuclei lie upon the very border of the mesoderm, and a few lie only partially within the epithelium. Fig. 10, *A* and *C* are repre-

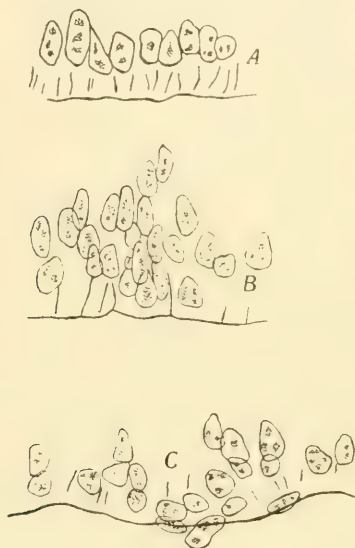


Fig. 10. Three sections of the olfactory epithelium of a 12 mm. swine embryo. *A* shows the nuclei in a row, located at a definite distance from the inner margin; *B*, nuclei that have moved slightly toward the mesodermal margin of the epithelium; *C*, nuclei in the act of migrating into the mesoderm from one of the elevations of the olfactory epithelium. $\times 533\frac{1}{3}$. Iron haematoxylin.

sentations of different portions of the epithelium of the same section. The general line of the nuclei lies about .00875 mm. from the margin, while, as shown in Fig. 10, *B*, some of the nuclei are within .0035 mm. of the mesodermal edge and in Fig. 10, *C* the nuclei lie directly at the mesodermal margin.

At the time the elevations appear, many cells, showing various stages of karyokinesis, are present. They are all lo-

cated near the outer margin of the epithelium. In a few cases in GOLGI preparations, central processes of neuroblasts were seen extending towards the brain wall into elevations of the epithelium (Fig. 7).

Formation of Connection between the Nasal Epithelium and the Brain Wall.—In slightly older embryos several cellular cords may be seen projecting a short distance into the mesoderm. The cords may be distinguished from the surrounding mesoderm by their compactness and their continuity with the epithelium. These cords are directed toward the brain (Fig. 11).



Fig. 11. Section of a 12 mm. embryo, showing the development of the "elevations" into short cords (*Cd*) projecting towards the brain wall. *F. B.*, wall of forebrain; *M.*, mesoblast; *N. P.*, lumen of nasal pit.

In embryos of twelve or thirteen millimeters length, these cords become much longer. As yet, there is no connection with the brain. In none of the specimens stained by iron haematoxylin, have fibers been observed. However, dissections

of embryos of this age show that the cords are firmly attached to the nasal epithelium and exhibit considerable tensile strength (Fig. 12). This can hardly be accounted for unless we grant that this cord is not purely cellular but somewhat fibrous in character.

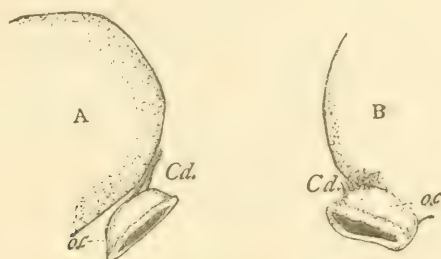


Fig. 12. Partial dissection of the head of a 12 mm. swine embryo, showing cords in the position of the future olfactory nerve, extending from the wall of the olfactory cup toward the brain. *o. c.*, olfactory cup; *Cd.*, cords; *A*, lateral view; *B*, lateral-dorsal view.

I have been unable to find, in addition to this peripheral anlage, any evidence of a cerebral anlage as has been described by BEARD for the selachians and CHIARUGI for mammals. Evidently, at least at this stage, the development is entirely from the epithelium.

At the time of the formation of the anlage of the olfactory nerve, the evagination of the forebrain to form the cerebral hemisphere is well under way. However, at this time, there is no indication of an olfactory lobe.

Establishment of the Olfactory Nerve.—In slightly older embryos, the cord may be traced to the brain. Dissections, as well as a study of serial sections, show clearly that many separate cords leave the epithelium (Fig. 14). I have counted fourteen on one side in one section (Fig. 13). These cords arise from various portions of the epithelium of the olfactory region. They run dorsally and slightly towards the mid-line. As they approach the brain, they converge to form a cellular mass, which, in later stages, appears as a kind of a cap over the end of the bulbus (Fig. 13). This cap remains chiefly cellular, even after the cord is almost completely fibrous.

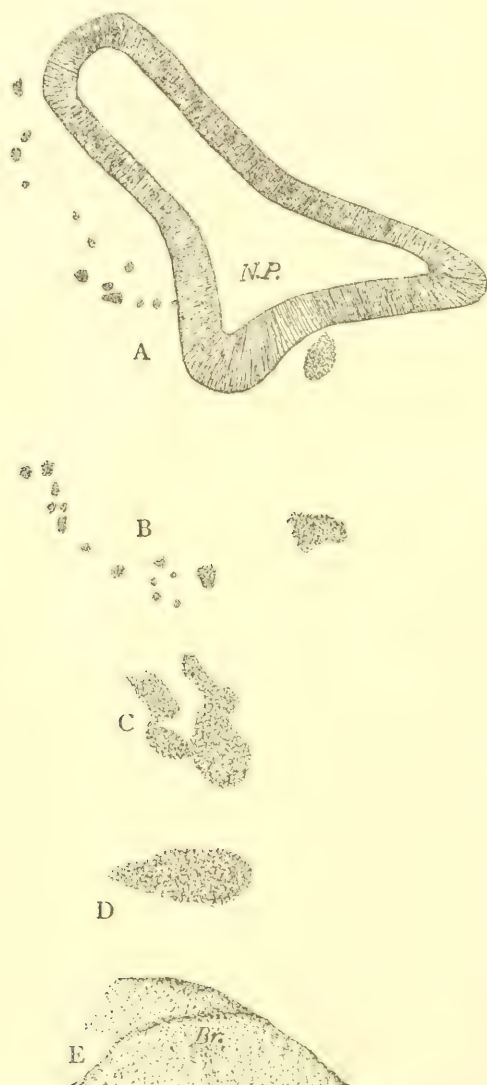


Fig. 13. A series of sections of the olfactory nerve of a swine embryo 14 mm. in length, to show convergence of cords into a cell mass which unites with the olfactory lobe. Thickness of each section $10\ \mu$. $\times 85$. *Br.*, Brain wall; *N. P.*, nasal pit.

B. $50\ \mu$ higher than A.

D. $110\ \mu$ higher than C.

C. $20\ \mu$ higher than B.

E. $40\ \mu$ higher than D.

In stages of eighteen millimeters and over, the olfactory nerve is seen to be double and is connected with the olfactory bulb by means of two roots, median and lateral, from each of which arise a number of filaments passing to the olfactory epi-



Fig. 14. Sagittal section of a swine embryo, 17 mm. in length, showing converging filaments (*fila olfactoria*) of the olfactory nerve. *O. L.*, olfactory lobe *N. E.*, nasal epithelium; *F. O.*, fila factoria; *C. M.*, cellular mass overlying the olfactory lobe. $\times 93\frac{1}{3}$.

thelium. These main divisions are apparently homologous to the two divisions described by many observers for the selachians.

Summary.

1. At the time of the formation of the olfactory plate, there is no trace of either cerebral hemispheres or olfactory lobes.
2. The olfactory plate shifts from a more dorsal to a more ventral position.

3. The nasal pit is formed by a process of invagination.

4. At a very early period in the formation of the pit, two kinds of cells are present in the olfactory membrane; first, columnar epithelial cells; second, spherical cells, located near the outer margin of the epithelium. Many of these latter cells are in the process of karyokinetic division.

5. These spherical cells develop into neuroblasts which, at first, are unipolar having only the central process developed, but later those which migrate from the outer margin become typical bipolar nerve cells.

6. For the most part, the developing nerve cells retain their position near the outer margin of the epithelium, but, in some cases, the cell body comes to lie at a deeper level within the epithelium necessitating the lengthening of the peripheral process.

7. Soon after the neuroblasts are formed cells from the inner part of the nasal epithelium push slightly into the mesoderm. This is indicated by a waviness of the margin of the epithelium, followed by distinct elevations extending towards the brain wall. Among the first indications of their outpushing, is a change in the arrangement of the nuclei of the cells of the epithelium.

8. Distinct projections extend from the epithelium into the mesoderm. While these projections are chiefly cellular, dissections show that they are also somewhat fibrous.

9. A few of these cells seem to be migrating neuroblasts, while the majority are evidently epithelial cells which upon being relieved of the pressure exerted upon them within the epithelium, take a more rounded shape.

10. These projections, which may now be known as cords, become much longer. They converge and near the brain unite to form a cellular mass, which, however, as yet, has no connection with the brain.

11. At no stage have structures been observed originating in the brain that may be considered to take part in the formation of the olfactory nerve.

12. In still older embryos, the cellular mass, to form which

the cords unite, is found to be in direct connection with the olfactory lobe of the brain forming a cap over the bulbus.

13. When established, the nerve is seen to consist of two portions, a lateral and a more median one.

From observations upon swine embryos, there seems to be no reason to question the peripheral origin of the cellular mass which is connected with the olfactory epithelium by cords, chiefly cellular. At no time, in the development, were any structures observed arising from the brain, which might contribute to the formation of this cell mass or to the cords.

MARSHALL, VON KÖLLIKER, BEARD, HIS, and others have considered these cellular structures to constitute the anlage of the olfactory nerve. That these cellular cords represent, in position, the olfactory filaments that arise later, there can be no doubt. Every stage can be traced from the first appearance of the cords as elevations of the epithelium up to the time of the presence of the olfactory filaments connecting the epithelium with the brain.

It is quite evident, however, that the majority of the cells of the cords are not the cells from which the olfactory fibers arise. The latter arise from cells the majority of which retain their original position within the olfactory epithelium. Only a few of the neuroblasts migrate from the epithelium. The central processes of the neuroblasts, located within the epithelium, are seen to be directed toward the cellular cords. In the chick, DISSE has been able to trace the processes into the developing cords and finally to the bulbus where they end in glomeruli. My preparations show also some neuroblasts in the act of migrating from the epithelium into the adjacent mesoderm. GOLGI preparations do not show within the bulbus any indication of the development of neuroblasts which send processes peripherally to form olfactory filaments. Since it is known that nerve fibers are continuous with only one nerve cell, we must conclude that the neuroblasts observed in the olfactory epithelium and which in some cases migrate into the mesoderm are the

cells of origin for the fila olfactoria. Consequently it must be affirmed that the olfactory nerve has a peripheral origin. This view is supported by observations made by EHRLICH,¹ RETZIUS,² GRASSI and CASTRONOVO,³ RAMÓN Y CAJAL,⁴ JAGODOWSKI⁵ and others upon the adult nasal epithelium of mammals and other animals.

The majority of the cells, therefore, that form the primitive cellular anlage of HIS and others do not develop into nerve cells. DISSE has suggested that they constitute the cellular sheath of the nerve, that is, are comparable to neuroglia cells. Their fate I have not been able to ascertain. The majority of them, however, accumulate in the cap formed over the end of the bulbus.

HIS's contention that this cellular anlage constitutes a true ganglion is not supported by my observations. My conclusions on this point harmonize with those of DISSE, arrived at for the chick. At most, there is only a partial formation of a ganglion located between the olfactory epithelium and the brain.

According to this view, the belief that the fibers of the olfactory nerve have the same relation to the olfactory cells as do fibers to sensory cells in the taste buds and tactile corpuscles is not tenable. The olfactory cells constitute the cell bodies of neurones of the first order.

¹ EHRLICH. Ueber die Methylenblaureaktion der lebenden Nervensubstanz. *Deutsche Med. Wochenschrift*, 1886.

² RETZIUS. G. Zur Kenntniss der Nervenendigungen in der Riechschleimhaut. *Biol. Untersuchungen*, Neue Folge, Bd. IV, 1892.

³ GRASSI and CASTRONOVO. Beitrag zur Kenntniss des Geruchsorgans des Hundes. *Archiv f. mikros. Anatomie*, Band XXXIV.

⁴ RAMÓN Y CAJAL. Origen y Terminacion de las fibras, nerviosas olfactorias. *Gazeta sanitaria municipal di Barcelona*, Dec., 1890.

⁵ JAGODOWSKI, K. P. Zur Frage nach der Endigung des Geruchsnerven bei der Knochenfische. *Anat. Anz.*, XIX, pp. 257-267.

THE RELATION OF THE CHORDA TYMPANI TO THE VISCERAL ARCHES IN MICROTUS.

By VICTOR E. EMMEL.

(Contributed from the Biological Laboratory of Pacific University, under the
direction of G. E. COGHILL).

The mammalian chorda tympani is a branch of the facial nerve which passes over the tympanic cavity, underneath the auditory ossicles and joins the lingual branch of the trigeminus. It is generally accepted that the tympanic cavity and auditory ossicles are derivatives of the spiracular cleft and visceral arches of fishes. It would seem a natural conclusion, therefore, that the chorda tympani is also homologous with the pre-spiracular branch of the facial nerve of fishes and amphibians. Upon this point, however, authorities are not agreed. On the one hand, a large number of investigators regard the chorda tympani as the homologue of the pre-spiracular (pre-trematic) nerve of fishes, as, for example, BALFOUR, in describing the anterior branch of the seventh nerve of Elasmobranchii, says: "This branch forms the prae-spiracular nerve of the adult and is homologous with the chorda tympani of mammals" (*Comparative Embryology*, Vol. II, p. 459). STRONG, in his work on the cranial nerves of Amphibia, interprets the r. mandibularis internus of fishes and Anura, and the r. alveolaris of Urodela, as homologous with the mammalian chorda tympani. On the other hand, DRÜNER denies that the r. alveolaris is the homologue of the chorda tympani (*Zool. Jahrb.*, XV, 3); while COGHILL, in his work on the cranial nerves of *Amblystoma*, interprets the r. alveolaris of Urodela as pre-spiracular, and takes the tentative position that the "most complete morphological and physiological representative (of the chorda tympani) in the

Ichthyopsida is probably found in the r. alveolaris of Urodela" (*Jour. Comp. Neurol.*, Vol. XII, p. 269). HERRICK questions whether STRONG's r. mandibularis internus in the homologue of the chorda tympani. He finds no nerve in *Menidia* homologous with the chorda tympani, and does not consider the r. pre-trematicus VII to be so homologous because it does not fuse with the r. mandibularis V and hence it does not distribute to the hyoid and mandibular arches in the way characteristic of mammals" (*Jour. Comp. Neurol.*, Vol. IX, p. 324). And finally, in addition to the r. palatinus, r. pre-trematicus and r. post-trematicus, STANNIUS, as cited by HERRICK (loc. cit.) describes in *Raja* and *Spinax* another branch of the seventh nerve which fulfills every condition for the chorda tympani. This conflict of opinion shows that the homology of the chorda tympani is far from being unquestionably established.

A chief source of this disagreement lies in the fact that the morphological relations of the chorda tympani to the spiracular cleft throughout the ontogeny of mammals is not completely understood. It has been accepted by leading authorities that the chorda tympani is a pre-spiracular nerve in the mammalian embryo. Very recently HERRICK in a literary notice of the work by VERSLUYS on "Die mittlere und aussere Ohrsphäre der Lacertilia und Rhynchocephalia" writes: "The detailed descriptions and figures make it very plain that the chorda tympani of reptiles is pretrematic and therefore morphologically pre-spiracular; and in the absence of very definite proof to the contrary, we must assume the same condition to prevail among the mammals also" (*Jour. Comp. Neurol.*, Vol. XIII, 1). LEWIS in giving "The Anatomy of a Twelve Millimeter Pig," says that the seventh nerve "divides into a pre-trematic and post-trematic branch, but the division is under the spiracle or auditory cleft and not over it as in fishes" (*Am. Jour. Anat.*, Vol. II, 2). In the last quotation it is not clear, however, whether by "division under the spiracle" it is meant that the chorda tympani itself passes over or under the spiracular cleft.

In the adult mammal the nerve in question clearly passes

over and in front of the tympanic cavity, so that, in view of the confusion of ideas as noted above, the question now is whether the pre-tympanic position is primary and maintained throughout the embryonic life, or whether it is a position secondarily acquired in the development of the tympanum. Of course, the further questions of homology cannot be settled till this point in mammalian embryology is determined. It was for the purpose of contributing something to the solution of this question that the following study in the embryology of *Microtus* was undertaken.

The embryos used in this study were killed and preserved in formalin. To insure a correct conception of the relations of the nerves to all parts of the head a model of a 2.3 mm. embryo, magnified 50 diameters, was made by the BORN method. Reproductions of two older embryos, also, were made by KASTCHENKO's method of graphic projection. My observations were made from the same series of serial sections as were employed for the model and projections, and from several other series of slightly different ages and cut in different planes.

First Embryo.

The youngest of the embryos was used for the construction of the model. The model and the sections from which it was made demonstrate clearly all the structures which are of importance for this study: the brain and all its flexures, the roots and ganglia of the fifth, seventh and eighth nerve, the mandibular and hyoid arches, and the posterior visceral arches as they are modified to form the sinus cervicalis. At this period the visceral arches are united only by a membrane composed of the two layers of epithelial cells, and the nerve trunks can be traced only a short distance into the mesenchyme of the arches.

Second Embryo.

From this embryo, more advanced than the first, two graphic projections were made, one of the exterior of the head and the other of the brain, fifth and seventh nerves and pharyngeal cavity. The mandibular and hyoid arches are still conspicuous

as typical visceral arches. The formation of the mandibular and hyoid cartilages has not begun, and these regions are filled with primitive mesenchyme cells.

*The Spiracular Cleft.*¹—In the dorsal part of the external groove between the mandibular and hyoid arches a small pit is found. From the apex of this pit the lumen of the spiracular cleft passes inwards and cephalad, and opens into the pharynx. Beginning in its most external part the lumen is very narrow for a distance of about .07 mm., then it broadens out into a flat cavity with its shortest diameter, as seen in the sagittal section, in a dorso-ventral direction. In the extreme lateral region of the cleft its epithelial walls approach each other in such a manner that the lumen is reduced to a small circular canal, until, finally, for an extremely short distance they come into close contact with each other, so that the lumen seems to be obliterated. *The epithelium of the cleft, however, is perfectly continuous with the epithelium of the skin.*

This relation of the visceral arches and the pharyngeal cavity to this cleft, and the continuity of the inner and outer epithelial plates are essential characteristics which establish its homology with the spiracular cleft of fishes.

The Chorda Tympani and Related Nerves.—The Gasserian, geniculate and auditory ganglia and their roots are clearly defined. The rr. ophthalmicus, maxillaris superior and maxillaris inferior are easily identified in their usual relations. Near its ganglion the r. maxillaris inferior gives off the buccal nerve, and, passing into the mandibular arch, divides to form the inferior dental and the lingual nerves. The latter can be traced into the base of the tongue.

From the geniculate ganglion the facial nerve passes outward and slightly caudad for some distance. Just back of the spiracular cleft it makes a slight turn ventrad. At this angle it gives off the chorda tympani from its anterior border. The

¹ The term *spiracular cleft* is used here as HERTWIG uses the term *sulcus tubo tympanicus*. This usage is justified by the relations as they are described farther on in this paper.

chorda tympani then passes directly forward *beneath* the spiracular cleft and close to its ventral edge. It soon turns inward and passes a considerable distance nearly parallel with the anterior wall of the cleft. Near the rudiment of the tongue it meets and fuses with the lingual brach of the trigeminus.

At this stage of the embryonic development of *Microtus*, therefore, the primitive continuity of the epithelium of the spiracular cleft and the skin still persists, and the chorda tympani passes behind and underneath the cleft and unites in a typical manner with the lingual nerve.

Third Embryo.

In the oldest of the three embryos, from which projections were made as from the second embryo, the pinna has begun to form, the mandibular and hyoid arches no longer appear as visceral arches and have assumed in a general way the adult conditions. The skeletal regions are still for the most part filled with mesenchyme cells, but the fundamentals of MECKEL'S cartilage and of the hyoid cartilage are distinguishable.

The Spiracular Cleft and External Auditory Meatus.—The comparatively large orifice of the external auditory meatus is bordered by the ridges or fundamentals of the pinna. The meatus soon narrows into a flattened cavity with its shortest diameter lying in the dorso-ventral plane, as seen in sagittal section. Its course is in a cephalo-ventral direction. It terminates as a blind tube. In a plane about .075 mm. outward from the blind end of the external auditory meatus, and dorsal of the meatus at a distance about equal to the greatest diameter of the meatus at this region, lies the blind end of the cleft which in the second embryo was identified as the spiracular. This cleft is also a flattened cavity with its longest diameter, as seen in sagittal section, lying in nearly the horizontal plane. It passes inward for a short distance, then takes a cephalo-ventral direction and opens into the pharynx. It is an important fact that in this embryo there is no continuity between the epithelium of the spiracular cleft and the skin.

The Chorda Tympani.—The ganglia and the main trunks

of the nerves are essentially the same as described for the second embryo. In addition to the inferior dental and lingual branches of the submaxillary, the mylo-hyoid and masseter branches are clearly defined. The lingual occupies a position along the inner side of MECKEL's cartilage and can be traced forward into the lateral region of the tongue. Of the facial nerve, also, the supra-maxillary and auriculo-temporal are easily traced in their usual positions. The chorda tympani is easily traced from its point of origin from the facial trunk. It passes behind MECKEL's cartilage, takes the same general direction that it does in the earlier embryo, and joins the lingual nerve near the point of separation of the latter from the inferior dental. But the relation of the chorda tympani to the spiracular cleft is distinctly different from that found in the earlier embryo. In its course in front of the hyoid cartilage and behind the proximal end of MECKEL's cartilage, it passes *over* the extreme lateral end of the spiracular cleft and close to its dorsal edge. It remains a question whether this lateral end of the spiracular cleft is the primary end of the cleft or a secondary evagination from it. It might be the latter, since it is generally accepted that the closed end of the cleft by evagination outward towards the external auditory meatus and upward around the chorda tympani and auditory ossicles, forms the tympanic cavity of the adult.

We find, then, at this stage of development that the chorda tympani no longer lies underneath the spiracular cleft but that it passes over the closed end of the cleft, or over the fundamen-
ment of the tympanum. This is the morphological position the nerve holds in the adult.

Conclusions.

The results of this study of the embryological development of the chorda tympani in *Microtus* lead to the following conclusions:

1. In the earlier stages of development the chorda tympani passes behind and underneath the spiracular cleft.
2. In

later stages this nerve occupies a position over and in front of the closed end of the spiracular cleft which is generally accepted to be the fundament of the tympanum. 3. The chorda tympani is, therefore, a post-spiracular nerve, and is to be considered as the homologue of a post-trematic nerve of fishes and amphibians.

EDITORIAL.

NATURE STUDY.

Energetic, enthusiastic and intelligent efforts are being made to introduce Nature Study into the American public school curriculum. The efforts themselves are not new, but enthusiasm and intelligence in connection with them perhaps are. HUXLEY's insistence upon the use of that which is vitally and practically related to human activities rather than conventional hereditary materials for the purposes of educational training, and AGASSIZ's pleas for the study of Nature before books are giving evidence of their influence.

With the year 1905 there will appear a journal devoted to Nature Study in the elementary schools. The founding of this, the *Nature Study Review*, is encouraging evidence of the recognition of the place and values of the study of Nature in our schools, and of the active interest of scientifically trained men. The editorial committee of the Review consists of L. H. BAILEY of Cornell University, H. W. FAIRBANKS of Berkeley, California, C. F. HODGE of Clark University, J. F. WOODHULL and M. A. BIGELOW of Teacher's College, New York City. These men, and such as they, are intelligently introducing the materials of natural science into our public schools. They are effecting just the kind of utilization of the materials of their own sciences that HUXLEY devoted so much of his energy and enthusiasm to encouraging. Grounded in genuine interest in scientific work as a source of knowledge which will promote the progress of the race, they are reaching beyond the narrowly circumscribed sphere of scientific investigation with the purpose of making Nature contribute directly to the education which is an important condition of human happiness and efficiency.

Perhaps no other book so well voices the judgment of those who stand close to the American school system as HODGE's *Nature Study and Life*.¹ It is a book which reveals the nature lover as well as the trained scientist in its author. It presents a sensible, highly practical scheme for the study of animals and plants in the graded school, while at the same time filling the reader with faith in the possibilities of the work for training, and with enthusiasm for Nature Study. Enter into the spirit of the life about you; do not live to search for truth, no matter what kind, but search for knowledge, understanding and sympathetic appreciation of Nature in order that life may be fuller, freer, and more nearly perfect—this is the injunction of the book. Learn to know the living beings as thoroughly as does the scientist, and to love and sympathize with them as he too often does not. There is inspiration for the reader in this book, for the author's faith in his cause and his enthusiasm are contagious. No one should read it who does not care to have his interest in Nature Study, both in and for itself and as a means of training the child, greatly increased.

Great depth of insight into the significance of the signs of the times in natural science is not necessary in order that one should be able to say that the next generation of Americans is to be a generation of naturalists. Interest in Nature is rapidly increasing and the introduction of Nature Study in the schools is now going to equip our future scientific specialists with an intimacy of acquaintance and sympathetic appreciation of Nature that will enable them to live the better and enter the more fully into the truth of their subjects. The important thing is that this general interest in Nature Study be made to contribute truly earnest investigators rather than dilettanti.

The study of animal behavior, of the life-histories, habits, instincts, and intelligence of organisms, of their relations to human industries, is only a small part of Nature Study, to be sure, but for those of us whose interests center about the func-

¹ C. F. HODGE. *Nature Study and Life*. Ginn & Company, Boston, 1902. \$1.50.

tions of the nervous system it is an important part. It is our duty to keep ourselves alive to the possibilities of adapting the results of our special investigations to the needs of Nature Study courses.

Furthermore, it is to our interest and for the good of our sciences that we make as much of our material available for the purposes of elementary training as possible, and that immediately, for thus will be implanted in the lives of those who are to advance scientific knowledge in the future a love of animals and a desire to know the truth that will lead them to constant and patient research.

When we thus in a journal devoted to pure science call attention to an apparently unrelated aspect of educational work and to a journal which is practical and pedagogical in its aims, it is not to be supposed that we are hopeful of direct contributions from Nature Study to pure science, but rather that we believe the introduction of the intelligent study of animals and plants into our elementary schools will indirectly and ultimately affect our scientific work importantly. What we are concerned about is that this shall be a desirable influence. That it will be desirable in many senses is guaranteed at present by the fact that men who know science in its research as well as its educational aspects are leading the Nature Study movement.

ROBERT M. YERKES.

RECENT CONTRIBUTIONS TO THE BODY-MIND CON- VERSY.¹

The present article does not attempt to review with any degree of completeness the field indicated by the title. Comprehensive digests have been given in the works by Professors STRONG and BUSSE quoted below and, to avoid misunderstanding, the writer desires to avow his purpose in advance, viz. 1) to submit to somewhat careful analysis the original view expressed in Dr. STRONG's book; 2) to bring into effective contrast therewith those statements of recent writers which may prove illuminating, and 3) to attempt a critical and constructive statement of the solution of this general problem offered by Dynamic Realism. By this frank avowal the reader may be prepared to excuse the anomaly that this paper may seem as much a pleading as a review.

At the outset we can do no less than express our hearty recognition of the merit of Dr. STRONG's work, which, for clearness of presentation, thoroughness of research, as well as candor and courage of treatment, is entirely admirable. Its usefulness will be especially apparent to those who find greatest difficulty in agreeing with all of the conclusions. It is assumed that the reader of these lines will also peruse the book and thus absolve us from the obligation of making a comprehensive digest of the contents, which consist so largely of the statement of conflicting theories as to leave too small space for a con-

¹ C. A. STRONG. *Why the Mind Has a Body.* New York, Macmillan, 1903.

LUDWIG BUSSE. *Geist und Körper.* Leipzig, 1903.

J. MARK BALDWIN. *Mind and Body from the Genetic Point of View.* Princeton Contributions, III, 2, Dec., 1903.

H. HEATH BAWDEN. *The Functional Theory of Parallelism.* Philos. Rev., XII, 3, 1903.

———. *Necessity from Standpoint of Scientific Method of a Reconstruction of the Ideas of Psychical and Physical.* Journ. Philos. Psych. Sci. Methods, I, 3, 1904.

HARTLEY B. ALEXANDER. *The Concept of Consciousness.* Journ. Philos. Psych. Sci. Methods, I, 5.

WILLIAM JAMES. *Human Immortality,* 1900.

W. OSTWALD. *The Philosophical Meaning of Energy.* Internat. Quart., VII, 2, 1903.

nected statement of the author's own position, which must, therefore, be assembled to a large extent from the critical portion of the work.

Professor STRONG classifies the theories, in so far as they are empirical, into

I. Interactionism: Psychophysical dualism and Psychophysical phenomenalism (interactionist type).

II. Automatism: Psychophysical materialism and Psychophysical phenomenalism (automatist type).

III. Parallelism: Psychophysical monism and Psychophysical idealism (the last being the author's position).

By the title chosen the author intentionally prepares his reader for the panpsychist view advocated, as he explains in the preface. For his theory he claims that "its difficulties are of the nature of obscurities, not of contradictions. Hence I think that panpsychists are justified in maintaining that with their principles they are able to explain the connection of mind and body." The author hopefully proposes "a settlement of the controversy between the parallelists and the interactionists," a hope which we fear few of his readers will be able to share.

The problem for the author, resolves itself into an "issue between interactionism and automatism, the former regarding the brain as an instrument used by the mind in dealing with the external world, while the latter conceives of brain-process as the physical basis or condition of consciousness, which simply accompanies the brain-process without exerting any influence upon it." One may argue with HUXLEY that consciousness is an effect of the brain-process, or with CLIFFORD that the two processes are parallel, the brain being no more responsible for consciousness than consciousness is for what happens in the brain.

In the introduction Professor STRONG effectively sets forth the results of the denial of casual relations which seems to be involved in any of these views. "Parallelism involves the denial of the physical efficiency of mind, and automatism the denial of its general efficiency." "Thus a whole series of scientific and philosophical conceptions of the first order—the principle of the conservation of energy, the mechanical theory of life, the biological doctrine of evolution, the philosophical conceptions of mechanism, efficiency, free will—all converge and come to a focus in the problem of the relation of mind and body. Not only so, but every one of these conceptions is vitally engaged, and will be found to stand or fall or suffer total transformation, according as we espouse interactionism, automatism, or parallelism."

We may reassure ourselves *sotto voce* that the case is not so bad as

it appears. We cannot agree that these are the only possible solutions of the problem, and we may add that any form of parallelism, *sensu stricto*, is simply an evasion of the issue. To say that brain-event and mind-event are cotemporaneous or consecutive is to offer no explanation of a fact of observation. It produces no scientific conviction that the next brain-event will be accompanied by a mind-event. It is no sense a theory—it is but a denial of the possibility of a theory. Many things that pass as parallelistic theories really go further and produce or assume a real tie between the two series, perhaps *via* some other element. This is especially true of functional theories. In the approach of the discussion of causation, which is evidently crucial in this connection, the necessity of determining what is meant by matter is encountered and frankly met: “For if at the present day there is a point on which philosophers show some approach to agreement it is that matter *does not exist*, in any such sense as the plain man supposes; that it has no existence independently of the mind.” We think that this statement is true only as to the first clause, or that the second statement is at least misleading. There are very few philosophers who would deny the existence independent of the mind of something corresponding to the concept of matter in the mind; certainly the author himself does not consistently do so and yet he will not carry all philosophers with him to the extreme of identifying the thing back of matter with mind as such. What philosophy and modern science tend so generally to agree upon is that the matter concept as such is erroneous in so far as it sets up a category of creation incongruous with all else in the universe and places it outside of the sphere of experience.

After spending forty-five pages in discussing “The Facts,” the author confesses that “In the course of this study, nothing has been established to the advantage or detriment of any particular casual theory. We carry away from it a single positive result: the law of psychophysical correlation.” This law states that consciousness as a whole never occurs except in connection with a brain-process, and that particular mental states never occur except in connection with particular brain-events. It would seem that important limitations may be necessary even in the application of this “law.” Brain processes must be taken in a very wide sense and the “mental states” of course refer to those of human experience and would not prejudice the possibility of “psychic modes” corresponding to other types of what may be called intrinsic aspects of other physical processes.

“Any view which ascribes physical action to the mind, no matter

what that action, can be reconciled with the principle of conservation of energy on the hypothesis that the mind is itself a form of energy." "The interactionist who shrinks from making consciousness a form of energy has, therefore, a single course left: to attack the universality of the principle of conservation directly." Here it is to be feared exists an unhappy confusion between consciousness and the extrinsic form of energy variously called "soul" or even "experience" (ALEXANDER) though Professor STRONG expressly says "the existence of consciousness is our existence. The soul is a dark and mysterious source from which consciousness in some unintelligible manner flows" though "insensibly we are drawn to picture it by the aid of that illegitimate notion of matter existing with all its materiality apart from consciousness—in short, as a mind-atom." What then are we to do with the whole infra-conscious part of life as well as the past unremembered stream of consciousness which we are wont to believe, with more reason than any other fact whatever, accounts for and makes intelligible the present consciousness? Such exclusion shuts us out from the teleology which alone accounts for our individuality upon the confession of idealists themselves. The idealist indeed holds "that we can have immediate knowledge only of our mental states;" to which the realist replies that this statement does violence to a fundamental dictum of science that with action there must be reaction. A purely spontaneous activity or energetic manifestation is impossible in a created universe (it would be a miracle and there are no miracles in philosophy, however it may be in theology). To say that my mind created reality out of nothing as a spontaneous fiat is to misapprehend the nature of reality. The fact that I experience a phenomenal universe demands something other than the simple subject of experience. For, as we like to say, reality is the affirmation of attribute and involves subject and object, energy and limitation, action and reaction, and so is *ipse facto* proof of extraneous somewhat. This reality does not necessarily vindicate our interpretation of it as object but it implies something to be interpreted. The author himself, however, provides a corrective in various places and admits that "the need in question (i. e., of explaining perceived events by means of preceding events not perceived) can only be met by some form of realism." "Though the objects themselves we perceive cannot continue to exist when we no longer perceive them, it is consistent with idealism that they should have extramental causes which continue to exist and of which the perceived objects are symbolic." Now if this be idealism it is idealism in terms of realism—an idealism with the sting extracted so that it is harmless

even to the most naive form of common sense. Later we somehow discover to our chagrin that this extra-mental something is also mental.

There will be pretty general agreement that, "if we come to admit things-in-themselves, we shall have to conceive them as non-material." But why in the same connection add that "If things-in-themselves exist, their existence cannot be immediately known, but only inferred. The broadest of distinctions separates such extra-mental realities, which in the nature of the case can never be immediately given, the hypothesis of which is consequently unverifiable, from the empirical objects, such as matter and motion, thoughts and feelings, *which we know by immediate experience*" (italics mine). This is most reasonably explained as a simple lapse but such lapses occur throughout. Surely Professor STRONG does not mean that an object is given in experience. Or, if he does, he cannot mean the metaphysical postulate of matter already admitted to be illegitimate, is known by immediate experience. If we know matter and motion by direct experience, that is the end of it. Is there no difference between knowledge and experience? Dynamic realism insists that we *know* external objects in the same indirect or secondary way that we know self. Genetic psychology traces the origin of both from an earlier "protoplasmic" condition of consciousness. The objective and subjective are both given in experience and the act of judgment (or intuition) recognizing an external object is as valid a process as that which recognizes the individual self. Experience gives us neither; all simple realities imply both but the partition is made in thought and gives us knowledge equally of the two elements. This individualizing peculiarity of human mind is implicate of limitation.

Professor STRONG, however, defines reality as "something which exists of itself and in its own right and not merely as a modification of something else." But would this not make the "Absolute" the only reality? for obviously only It can exist "of itself." But this necessary result is not perceived by the author and to some extent will go far to invalidate the chapter on consciousness, etc.

The distinction made between soul and self is interesting and suggestive. Soul is a metaphysical entity back of self much as some entity exists behind matter. Mind and soul are two different conceptions, the former corresponding to the soul of empirical psychology. "Consciousness is empirically a thing so mutable and transitory that we cannot conceive it except as supported by some more durable underlying being, and our choice lies between making it dependent on the brain and on the soul," and "since the brain, as material, cannot treasure up what

is spiritual, the treasure-house must be the soul." It seems quite impossible for this writer to escape from the nave form of materialism in his discussion. In spite of his explicit statement of the non-existence of matter, he everywhere sees it as assumed till he, by its destruction, has proved his triumphant point. He says: "As there cannot be motion without an object to move, so there cannot be thought without a thinker." But this is a false analogy. The "object" which moves exists only as a judgment compounded of varieties of activities. So far as physical science knows, the movements of an object is the moving of other sorts of movement. In other words, we simply establish relations between different orders of activities or energetic complexes.

In the course of the chapter devoted to the possibility of "things-in-themselves," after stating that no argument from analogy can possibly prove the existence of things extra-mental, "The utmost it can do is to indicate their nature, when their existence is known from some other source," and "it is in the nature of the case, impossible that consciousness should supply rational grounds for the inference of realities beyond itself." Dr. STRONG goes on to state as a categorical and "striking fact" that something to which neither the external nor the internal senses lend the slightest testimony may yet with perfect certainty be known to exist." It is to him a matter of surprise "that it never occurred them (all other philosophers) that we might have a kind of knowledge less rational than either, a kind founded on neither reason nor experience, but solely on instinct. It never occurred to them that neither experience nor reason can fully account for the knowledge of other minds." How this is made to agree with a later statement that "through our mental states, which alone are immediately given, we may obtain knowledge of non-empirical existences, as we see in the case of other minds," we must leave to the author.

A different point of view sometimes appears, as where it is said "The reality of an object signifies its membership in an order in space and time existing for all similarly organized percipients."

As to Professor STRONG's distinction between brain process and mind process, the former a possibility of perception, the latter forever beyond it (transcendent), it must be remembered that the distinction is made in our own experience before it can be predicated of another. So far as the mind process of another becomes knowledge it is inferred in exactly the same way that brain process is, but we project the subject-object dualism of experience into another.

As DEWEY remarked in a recent lecture, "states of consciousness have been made either a mythological monster eating up the whole of

reality (subjective idealism)—panpsychism, or the other way is to say that atoms and molecules are the real thing and states of consciousness only an accidental phosphorescence or epiphenomena." "Mental states are not different stuff from the objects, but the attitudes, the individual attitudes, necessary for reconstruction of the experience and thus the counterpart of the objects in this process of construction. The subjective is real, as an attitude, etc."

Coming finally to the author's statement of the Psychophysical Idealism for which the book stands, it reduces to the statement that "brain-process is a manifestation of the accompanying mind." The mind is manifested directly through the brain. We have supposed that our thoughts are given directly; but not so, we only know we think when we discover changes in the brain cortex. But we would not do the author injustice. We are now astonished to discover that "by brain event we mean the actual modification of another or the same consciousness—and this is the only natural or strictly defensible meaning of the word." This identification of brain-event and mind-event would seem to reduce the matter to a question of identity and we might have been spared the rest of the book. (Yet in the next sentence we return to "nerve currents passing from eye to brain" and "perception of the brain event").

Behind a mass of contradictory and inconsequent statements we frequently get glimpses of a genuine realism. "The phenomenal causal relation between sensory stimulus and sensational brain event is the symbol of a real causal relation between the extramental event and the sensation, the phenomenal causal relation between the volitional brain event and voluntary motion the symbol of a real causal relation between volition and an extra-mental event." The link between this idealism and modern realism must be found, we believe, in the interpretation of energy as potentially capable of mentality as a manifestation of all or some of its modes. In this sense the two systems agree in holding "the universe to be in all parts mental in nature."

Panpsychism will offend the scientific mind by what seems an unwarrantable assumption that all things in themselves are mental in their nature. They will ask with Professor STUMPF "How can we conceive of a crystal, a dew drop, or a molecule as possessing anything analogous to sensation and will as we know them in ourselves?" This difficulty Dynamic Realism meets by assuming a unitary nature underlying all things. They have in common an energetic character which implies, on the face of it, nothing more than efficiency or power to act, and this, of course, a fundamental philosophical necessity of all

being. The individualizing character is *mode*. There is the widest variety and there are compatibles and non-compatibles among modes. There is for each unit (complex, energetic center) a form peculiarly its own to which there attaches an intrinsic as well as an extrinsic value (action and reaction). The intrinsic value would be a "genetic mode" incapable of being translated directly in terms of any other kind of being (but about which descriptions may be formulated in psychological language). This is revealable directly only in itself but is the condition of the reflection of the external world into self. Such a mode is every form of consciousness, instinct, affinity, habit, attraction (and what-not unknown to us in the lower types of energetic centres). There is no such thing as a general consciousness, only various conscious modes. The line between the conscious and unconscious in the intrinsic sphere is vague. In its earlier simpler form consciousness may be but a longing, instinct, impulse or attraction. Each such genetic mode is the intrinsic side of a definite kind or form of energy which is also capable of becoming an object of observation extrinsically by influencing other energetic centres.

The real self in the case of man is not the sum of his conscious acts at any one time or all times, nor of his bodily activities, but the energetic complex which, viewed intrinsically, forms the one, and viewed extrinsically forms the other. The real self is the "metaphysical soul" referred to by Dr. STRONG which is not only panpsychical but panphysical.

In this connection it is interesting to trace with Professor BALDWIN genetically the origin of *ideas* of mind and body. Assuming that experience is at first protoplasmic or undifferentiated, the first distinctions are of the "projective" order and do not give us self and not-self as usually stated, but persons and things. Self is recognized later and is divided into a body part and mind part.

It is also important to consider that the "procedure which involves treating other minds as objective phenomena, and at the same time maintaining the psychic point of view with reference to one's own mind is illegitimate." "The fallacy of the subjectivists is in saying that in contrasting body and mind we may mean the thought of a body which is a constructed object subject to analysis, and a thought of mind which is not an object at all." (Of this fallacy the work entitled "Why the Mind has a Body" is an illustration, as already pointed out.)

The fallacy of the materialists, according to Professor BALDWIN, has its roots in "taking the spontaneous standpoint for one term of

the antithesis, body, and the reflective standpoint for the other, mind." The nature of Professor BALDWIN's answer to the question: "How can body and mind, being what we have come to think them to be, live hospitably housed together in one phenomenal group of facts?" is only vaguely foreshadowed under the term, "Esthonomic Idealism" and the "hope for a theory of correlation" is precisely what inspires the dynamic realist in the energetic postulate.

We cordially assent to Dr. ALEXANDER's criticism (*Op. cit.*) of JAMES' "stream of consciousness" which he wishes had never been invented, for "It could hardly have arisen except in connection with a parallelist, psychological view, and in metaphysics it is certainly harmful." For the rest, the most important point in ALEXANDER's article is his discrimination of experience and consciousness. "Experience means just the as yet unanalyzed and unclassified facts and happenings encountered in the course of a natural human life." But this is not the usual view; it implies a soul other than the mind corresponding to the "life" or complete being of the dynamic school, or, as LOTZE would say, "the life of a soul," coming into intelligibility in consciousness. Consciousness is only an illumination of experience and it may be a very partial illumination. The very appreciative allusion to Professor MACH's view is interesting, for MACH, more than most writers, solves the puzzle by denying its existence, stating that, in last resort, the data of physics and of psychology are the same. But (inconsequently, as it seems to us) Professor ALEXANDER seems to imply that we have a means of knowing certain realities to be "wholly inanimate and quite unconscious."

Professor BAWDEN's earlier paper, "The Functional Theory of Parallelism," also quotes with approval MACH's view that "the boundary line between the physical and the psychical is solely practical and conventional." "I see, therefore, no opposition of physical and psychical, but simply identity. In the sensory sphere of my consciousness everything is at once physical and psychical." Professor BAWDEN considers that "the mental life is a continual synthetic construction. It is simply the name for the orderly continuous functioning of an organism under conditions of tension in adaptation." "Mind is not an entity behind the process of consciousness; it is that process itself."

In several places the materialistic view is verbally allowed, as where the statement is made that "mind is here viewed as the totality of the functioning matter." But "The psychical is the *meaning* of the physical." "Consciousness represents what, comparatively, we may call the tensional equilibrium of the organism, whereas habit represents its relatively stable equilibrium."

It would appear, therefore, that a man is a whole both to the child and to the philosopher, but to the psychologist who stands between, there exists the dualism of mind and body. "It appears a problem only because of the fact that our experience is not yet completed, that, as Professor BALDWIN says, it still has a career before it."

In a later paper (*The Necessity from the Standpoint, etc.*) Professor BAWDEN states the energetic view, "Under the name of energy, motion is now regarded as itself the essence of reality, and the idea of brute, lump matter drops away. In place of the static we get the dynamic theory of the nature of reality." "This is the dynamic or energist's view quite generally held by philosophical physicists today." "The solution of the paradox (that time is built up in consciousness while the latter is an evolution in time) lies in seeing that consciousness, taken apart from the organism which is conscious, is not an entity or thing or even a process, it is only a meaning or significance." A meaning to what or whom? To the organism? Professor BAWDEN claims that the dualism of consciousness and organism is simply methodological not ontological. "Consciousness is not an entity or thing; it is a function, a meaning." But if the being of the organism be its activity, consciousness resolves into the function of an activity and we reach a conclusion like that of MACH referred to. In fact, the word *function* is perhaps unfortunate and could hardly be used in a strict way if we held to a materialistic construction of physical being. Evidently by "function" is not meant the doing that constitutes the being of things, but the interpretation of this doing or its revelation in the act of doing. It would seem to be nearer the conception intended by all the writers last mentioned if we conceive of energy or activity as the ground of all being and admit that the specific *meaning* of each form depends on its mode, form or type. Each type has its intrinsic meaning, but whether it shall be what we call consciousness or not depends on the exact form which the energy assumes.

This sketch would be incomplete without reference to Professor JAMES "Barrier Theory" of mind. It would interesting to know how far the author was influenced by his well-known leaning toward occultism and the mystical in general in putting forth this theory. Starting from the statement (to which we are asked to subscribe in advance) of the "great psychophysical formula: Thought is a function of the brain," Professor JAMES considers that the difficulty so generally felt in the acceptance of this statement is due to an unnecessary limitation in the meaning of the word "function."

Professor JAMES thinks that, when we speak of the power of the functioning of a moving waterfall, etc., "the material objects have the function of creating or engendering their effects and their function must be called productive function." But we also have releasing or permissive functions and we have transmissive functions. "When we think of the law that thought is a function of the brain, we are not required to think of productive function only; we are entitled also to consider permissive or transmissive function." The universe of material things may be but a surface-veil of phenomena, hiding and keeping back the world of genuine relations. Our brains are half-transparent places in the veil. The genuine reality, the life of souls as it is in its fulness, will break through our several brains in all sorts of restricted forms, with all the imperfections and queernesses that characterize our finite individualities here below. Through the weak spot in us, namely, our brains (appropriate conception) "Gleams, however finite and unsatisfying, of the absolute life of the universe, are from time to time vouchsafed. Glows of feeling, glimpses of insight, and streams of knowledge and perception float into our finite world." Those writers who envy Professor JAMES his superb mastery of English style may piously express their gratitude that they escape the temptation to sin with impunity against logic which that mastery confers. It is hard to think at the same time in tropes and syllogisms.

The forms of consciousness (thoughts, etc.) are either predetermined before they leave the great universal sea of all consciousness or else they are individualized and determined by the nature of the hole through which they pass. If the former, there is some determinant either in that sea or between it and the brain. But evidently Professor JAMES believes the brain to be the determinant for he uses the figure of the glottis determining the sounds by limiting air currents passing through it. Only on this presumption could the thoughts be ours. Only on this theory could there be any explanation of the curious fact that we have brain at all. But on this assumption the brain has just as productive a function as any in the world. Surely no one, unless it be some kind of a panpsychist, contends that new energy is created by thinking. The figure of the water power used by JAMES aptly illustrates this. The form of the aperture in the turbine determines (produces) the modification of energy constituting the work of the mill. The waterfall "creates or engenders its effects" only by modifying the form of existing energy. Creation itself is only such a modification (self-limitation). The difference between a productive and permissive function is a play of words only.

C. L. HERRICK.

LITERARY NOTICES.

His, W. Entwicklung des menschlichen Gehirns während der ersten Monate.
Leipzig, S. Hirzel, 1904. Price M. 12.

Neurologists are to be congratulated that before his death Professor His was able to bring the present work to completion—a beautifully illustrated volume of 176 pages. After the appearance of his paper on the development of the medulla oblongata the publication of this series of researches was interrupted, as the author tells us in the preface of the present work, during the period of active reconstruction of morphological conceptions represented by the labors of FLECHSIG, GOLGI, RAMÓN Y CAJAL, etc. In the meantime Professor His had been continuing his investigations and now at the close of the research period just referred to presents an installment which covers the histogenesis and morphogenesis of the entire central nervous system in its earlier stages, including a revised summary of much that is contained in the earlier papers.

In the review of the histogenesis of the nerve tube, the term syncytium is applied for the first time, I believe (p. 13), to the spongioblastic framework as it appears in the earliest form of the “*Randschlier*”—a conception which has been abundantly confirmed and enlarged by HARDESTY in his latest contribution. He abandons his former view that mesodermal elements enter with the blood vessels and share in the formation of neuroglia, while HARDESTY, in the work just cited, admits a still more extensive participation of mesoderm in the neuroglia by means of a fusion of the spongioblastic syncytium with the enveloping connective tissue syncytium.

The germinative cells are again described as a distinct category, though from the brief reference it appears that, as contended by recent critics, they are probably nothing other than undifferentiated cells in a state of mitosis. For the recognition of neuroblasts there is no criterion save their connection with a nervous process (p. 21).

The section devoted to the longitudinal zones of the central nervous system is disappointingly brief. Recognizing the inadequacy of the original terms basal plate (*Grundplatte*) and alar plate (*Flügelplatte*),

it is proposed to substitute the terms hypencephalic area (including the hypothalamus, etc.) and epencephalic area (cerebral and cerebellar hemispheres, thalamus, corpora quadrigemina, brachium conjunctivum, olive and part of the pontile nuclei).

HIS combats vigorously (p. 29, ff.) the idea of the origin of conduction paths from a primitive nervous syncytium as expressed by BETHE in his recent book.

Summarizing the development of the brain in the first month, we find that the regional differentiation of the medullary tube is begun, but not far advanced. There is formed a separate mantle layer containing neuroblasts whose neurites form motor root fibers, arcuate fibers and in the ventral zones longitudinal funicles directed caudad into the spinal cord.

The chapter on the development of the cerebral hemispheres comprises 96 pages. The earlier contributions on the form relations are reviewed and thoroughly worked over. The histogenesis of the cerebral cortex as it occurs during the third and fourth months is given in detail, followed by the development of the blood vessels and commissures. Finally, 75 pages are devoted to the sequence of development of the intra-medullary fiber pathways.

C. J. H.

Wilder, Burt G. The Brain of the Sheep. *Physiology Practicum*, Part IV, pp. 49-76. Published by the Author, 1904.

A copy of the latest revision of Dr. BURT G. WILDER'S Practicum devoted to "The Brain of the Sheep," indicates that this veteran neurologist is still employing the familiar methods which have served so good a purpose in his hands. The revision chiefly concerns details and the author cannot refuse a plaintive yet hopeful protest against a "reactionary tendency" as regards nomenclature in America.

C. L. H.

Harrison, Ross Granville. Experimentelle Untersuchungen über die Entwicklung der Sinnesorgane der Seitenlinie bei den Amphibien. *Archiv f. mik. Anat.*, Bd. LXIII, H. 1, pp. 35-149, 1903.

The results of numerous cutting and grafting experiments performed upon frog embryos at the time of the growth of the lateral lines show that the lateral line *Anlage* follows definite paths formed by the surrounding tissues, that its growth is determined by forces within itself and not from stimuli received from surrounding tissues, and that the differentiation of the *Anlage* into the sensory and supporting cells of the sense organs is likewise free from the influence of the surroundings except that adequate space is necessary for the development of typical organs.

J. B. J.

Mills, C. K. The Physiological Areas and Centers of the Cerebral Cortex of Man, with New Diagrammatic Schemes. *Univ. of Penna. Medical Bulletin*, XVII, 3, pp. 90-98, May, 1904.

The history and theory of cortical localization are briefly reviewed and the new features of the author's diagrams commented upon.

C. J. H.

McCarthy, D. J. The Formation of Bone Tissue within the Brain Substance. A Contribution to the Inclusion Theory of Tumor Formation. *Univ. of Penna. Medical Bulletin*, XVII, 3, pp. 120-121, May, 1904.

Report of a small tumor containing true bone tissue which appeared in the cerebral hemisphere of a young cat subsequent to an experimental lesion.

C. J. H.

Piper, H. Das elektromotorische Verhalten der Retina bei *Eledone moschata*. *Archiv für Anatomie und Physiologie*, pp. 453-474, 1904.

The author starts out from the observation that water, and especially the water of the Mediterranean Ocean, strongly absorbs red and yellow rays of light so that the sunlight which reaches moderate depths below the surface is strongly tinged with blue and green. HIMSTEDT and NAGEL had discovered in 1901 that the action currents of the frog's retina are stronger for intense yellow light (natrium) than for any other intense colored stimulations which they applied. Now the yellow portion of the solar spectrum as measured bolometrically has a greater energy than any other part, so that these authors referred the greater action currents for yellow light to an economical adaptation of nature, whereby the light most predominant in nature has also the greatest stimulation value. The human eye receives the most intense sensation from the yellow part of the spectrum, so that they further concluded that the action currents of the retina are a fair measure of the intensity of the sensation being carried to the brain. And in confirmation of this they actually discovered that a frog's retina when adapted to "rod vision" before being removed, would then give greater action currents for blue-yellow light than for the yellow light to which the unadapted retina best responds; just as the human adapted eye sees the blue-yellow part of the spectrum as brightest (PURKINJE phenomenon).

Now Dr. PIPER inquires whether animals living some distance below the level of the sea will give the strongest retinal action currents for that color of light to which they are most exposed; and more particularly, whether animals living in the depths of the Mediterranean Ocean will have the strongest retinal currents for that blue light by which they are always surrounded. In fact, the author finds this to

be the case with the Cephalopod *Eledone moschata*. He demonstrates this admirably by tables and curves. Whereas the action currents of the frog's retina, for he was careful himself to repeat the experiments of HIMSTEDT and NAGEL, are the greatest for spectral light of about $590\ \mu\mu$ wave-length (yellow), those of the cephalopod's retina are greatest around the wave-length $500\ \mu\mu$ (blue-green). For considerably weaker intensities of light the frog's retina gave the strongest currents for the wave-length $560\ \mu\mu$ (yellow-green); that is, when the retina was more less adapted to darkness the position of maximum currents shifted from the yellow toward the yellow-green. This is in precise agreement with HIMSTEDT and NAGEL.

For both animals the author used a dispersion spectrum from the NERNST lamp; and he bases his conclusions on experiments with 13 specimens of *E. moschata*. In view of the extreme similarity of the results from the several individuals, this number seems quite sufficient to establish the author's point. The author used this species alone, because it was the only one which could be easily obtained and of which the eye on being removed retains vitality enough to make experimentation possible. It is interesting to note that the action current both attains its maximum and subsides very rapidly. Dr. PIPER does not confirm the results of BECK as regards the direction of the action current.

The paper is written with exemplary clearness and conciseness, and cannot fail to convince the careful reader; and this the more in view of the rare and delightful modesty with which the author claims to have established his interesting and important point.

E. B. H.

Keeble, Frederick, and Gamble, F. W. The Color-Physiology of Higher Crustacea. *Phil. Trans. Roy. Soc. London*, Ser. B, Vol. 196, pp. 295-388, 1904.

Notwithstanding the fact that color patterns and color changes have always interested naturalists greatly, and that much has been written concerning "protective" coloration and "color mimicry," it is only recently that color phenomena in animals have been subjected to any very close and accurate scientific investigation, looking toward an explanation of their origin. The work of STEINACH, RABL and CHUN on mollusks, and of KEEBLE and GAMBLE on Crustacea not only clears up many points that were uncertain before, but will also doubtless stimulate to further investigation in a field of inquiry that promises to be most fruitful.

The present monograph by KEEBLE and GAMBLE is one which de-

lights the eye by the excellence of its form and arrangement, and rejoices the heart with the thoroughness and accuracy of the work and the far-reaching importance of its results. It is really a continuation and amplification of the investigation by the same authors on "Hippolyte varians: a study in color-change",¹ extending the observations made on this species and including a study of *Crangon*, *Palaemon*, *Carcinus*, *Portunus* and *Galathea*, based upon *Macromysis* as a fundamental type.

In *Macromysis* the authors observe that the color units, the chromatophores, are arranged in three main groups and one accessory group. The three main groups are (1) the neural, in relation to the brain and nerve-cord; (2) the visceral, connected with the alimentary tract, liver and gonad; (3) the caudal group on the upper surface of the tail. These three groups are so related that they may be conceived as forming a system, the *primary system of chromatophores*. The accessory group, on the other hand, is related to outlying structures, and may be considered as an *incipient accessory system*. The chromatophores are not simple cells, as they are widely considered, but consist of a protoplasmic, pigmented center, enclosed in a spherical thin-walled bag, which is pierced by the proximal ends of a number of cells varying from five to nine. These cells have their nuclei in, or close to, the chromatophore center, and extend outward in branched, fibrillated processes, the whole being not unlike the branching of a tree. Some of these branches are 2 mm. and over in length.

The chromatophore centers of *Macromysis* contain two kinds of pigments, a brown pigment, which turns red and is finally decolorized under the influence of oxydizing agents, and a small quantity of pigment which is bright yellow or white by reflected light, but has a grayish color in transmitted light. It is the brown pigment that gives the characteristic color pattern to the animals, giving them a dark brown tint when expanded, i. e., when the pigment migrates to the branches, and leaving them colorless or gray when the pigment contracts to the center.

In decapod Crustacea the situation is much more complex. The color-marking of the adult decapod is determined by the development of the secondary system of chromatophores, which completely covers up the first and differs from it in having much shorter branchings and being much more decentralized. In the larval stages, however, through the Mysis stage, the primary system remains in the ascend-

¹ Keeble, Frederick, and Gamble, F. W. Hippolyte varians: a Study in Color-change. *Quart. Journ. Micros. Science*, Vol. 43, pp. 589-698, 1900.

ency, so that the larva is more like *Macromysis* than it is like the adult form. This primary system persists unchanged in the adult but is overlaid by a secondary, and sometimes even by a tertiary, system of chromatophores. The pigments of this secondary system are either absorbing or reflecting; the former, red, yellow, brown, violet and diffuse blue, are the same in transmitted and reflected light, the latter are only effective in reflected light, and appear white, yellow, greenish or blue, as the case may be.

The question is raised whether these chromatophore systems and the color patterns resulting from them are inherited or acquired. After marshalling the evidence the authors conclude that the primary system, owing to its appearance in the earliest larval stages, and its persistence in the adult, is inherited in all cases. In *Crangon* and *Palaeomon* there is a steady, constant development of the secondary pattern from the embryo to the adult, and hence the secondary system is thought to be inherited in these forms. In *Hippolyte*, however, there does not seem to be any such constancy of development, but the dominant color-pattern is rather a result of the action of the environment.

Regarding the mechanism of pigment migration the authors hesitate to express themselves. They are not inclined, however, to accept POCHET's view that it is due to the active amoeboid movement of cell processes, but prefer to account for it by the turgidity of the constituent cells of the centers, caused chiefly by the action of light, and controlled to a greater or less extent by the nervous system. This view is strengthened by the fact that in old *Mysids* "the pigment at times bursts the frondose extremities of the chromatophores and exudes into the surrounding tissues." Moreover, the origin of the chromatophores is to be found, not in connective, but in glandular tissue, and their action seems to be like that of a gland, continually secreting or transforming pigment substances.

In *Hippolyte varians* there is a regular alternation of the diurnal color-pattern, due to red and yellow pigments, with the nocturnal, which is blue. Under appropriate light stimulation the red and yellow pigments flow out through the branches, and when the stimulation is withdrawn, these pigments contract and there is a diffusion of blue. The authors think, however, that the blue pigment does not serve any protective purpose, but is rather a by-product obtained by the transformation of the yellow and red pigments, and "exudes from the chromatophores, permeates the tissues and subsequently disappears."

Perhaps the most interesting portion of the paper is the last section, which deals with the influence of light on littoral Crustacea.

During the day *Palacmon* and *Hippolyte* are quiet and sluggish, but in the evening they become very active and restless, many throwing themselves out of the shallow pans in which they are kept. Hence the authors think that these animals should be considered nocturnal. Experiments on phototropic reactions (going toward or away from the light) showed that the animals experimented on formed a series, *Palacmon* being negatively phototropic (light-shunning), *Hippolyte* positive (light-seeking), and *Macromysis* negative on a white ground but positive on a black ground. The zoeae of *Palacmon*, however, are positive, and if given a choice of ground select the white. The adult *Palacmon* and *Macromysis* choose the black, while *Hippolyte* in all stages prefers the white. A test was made to determine whether the positively thigmotropic *Palacmon* could be driven from the bottom of a bottle, whose upper portion was darkened, by its negative phototropism. As long as there was nothing in the upper part of the bottle to cling to, the animal returned to the bottom after a short swim above. When an inclined stick was placed in the upper end of the bottle, *Palacmon* remained clinging to it in the shadow.

The effect of light upon pigment migration is discussed in great detail. The effect of light stimulation was found to be in part direct, and in part indirect, i. e. through the eyes and the nervous system. The indirect response is the most important for color display, but its action is slower, so that the direct response often gets a start, and then is checked by the indirect. The direct response is determined not by the background but by the incident light, whereas the indirect response is determined by the background entirely, a white ground causing contraction of pigments, and a black ground expansion. "There is a close agreement between the phototropic reaction and the pigment-movement reaction; both depend on the eye and both are determined by 'background'".

"A monochromatic light in conjunction with a scattering (white) or absorbing (black) background, produces the same ultimate effect on pigment movement as does a white light in conjunction with the same background. The fact of background must be taken into consideration in all experiments on phototropism."

In conclusion let it be said that the work is well supplied with summaries, an appendix of 17 tables, a bibliography of 62 numbers and seven splendid plates.

J. CARLETON BELL.

Porter, James P. A Preliminary Study of the Psychology of the English Sparrow. *Amer. Jour. Psychology*, Vol. XV, pp. 313-346, 1904.

As the author remarks, the psychology of the sparrow is of special interest because of the remarkable degree of success which this bird has attained in its struggle for existence in America. If adaptability is taken as a measure of intelligence the sparrow certainly ranks well in the psychic scale.

PORTER'S preliminary paper is characterized by admirable clearness and accuracy of statement. His experiments are thoroughly scientific in plan and execution, and his results, although as yet limited to only one or two individuals, are as valuable as they are interesting.

The present paper contains observations on general behavior and characteristics, and reports of experiments to test association and perception of number, form, color and design.

The association tests, with food boxes and a maze, indicate that the bird is able to profit by experience very rapidly. In fact the habit curve given by the author's tests is strikingly like those of the rat and monkey. The sparrow evidently learns by trial and error; there is some evidence of imitation, but "no sign of reason or looking ahead and suiting of means to an end." There is notable persistency in the efforts to obtain food, whether it be by opening the door of a food box or finding the way through a maze. Memory appears to be good.

There is evidence of perception of number similar to that of monkeys. As the author suggests this may be "sense of position" rather than "sense of number." The few experiments described indicate little ability to distinguish forms; but colors and designs were distinguished readily by the single individual tested.

A comparative study of bird psychology is promised by PORTER as a continuation of this preliminary paper. R. M. Y.

Uexküll, J. v. Studien über den Tonus. II. Die Bewegungen der Schlangen Sterne. *Zeitschrift f. Biologie*, Bd. 46, 1904.

This paper is noteworthy as evidence of the value of kinematographic photography in the study of animal reactions. The author succeeded in obtaining series of photographs of the serpent star (*Ophioglypha lacer-tosa*) which show splendidly the manner of locomotion, of turning over, of taking food, of freeing members from encumbrances, etc. One is able to see clearly in these series of pictures the different phases of movement, and to determine precisely what part each member plays in the reaction, as well as the way in which the movements of the parts are coördinated.

In addition to descriptions of the normal activities of the organ-

ism v. UENKÜLL gives accounts of certain experiments which had to do with food taking and various forms of behavior which are apparently intelligent, and with the forms of reaction of one, two, three or four armed animals.

The descriptions of the reactions, which cannot be summarized within the few sentences of this notice, are followed by a consideration of the structure of the animal in its relation to reaction. The mechanics of movement are discussed. In connection with an examination of the principles of action in the nervous system the author takes occasion to show that the nerve impulse always passes in the direction of the expanded muscle (p. 28). The paper is a valuable contribution to our knowledge of the workings of the nervous and muscular systems in this form.

Considering the great possibilities of the kinematographic method for the investigation of reactions and their reproductions on paper or on a screen, it is surprising that it is not more widely used. Photographs taken at the rate of 20 to 30 per second make possible the careful analysis of movements which are too rapid for the naked eye to follow satisfactorily. Moreover, a series of photographs will often make clear at a glance what pages of description may fail to make intelligible.

R. M. Y.

Binet, A. *L'Année Psychologique*. Tenth year, 1904. Paris, Masson et Cie, Editeurs.

The tenth issue of the *Année* contains the Bibliography for 1903 (about 3000 titles) and the annual abstracts of the more important works. The original memoirs include several of interest to our readers, notably the paper by LECAILLON, "La biologie et la psychologie d'un araignée" and ZWAARDEMAKER'S "Sur la sensibilité de l'oreille aux différentes hauteurs des sons." Besides these features, we have the announcement of systematic annual digests of cytology, anatomy, physiology, pathology, anthropology and a number of other collateral fields, each by a specialist, which promise to be of great value. Twelve such digests are given in this issue. Attention should be called to the fact that the publisher of the *Année* has been changed since the last issue.

C. J. H.

Smallwood, W. M. Notes on the Natural History of Some of the Nudi-branches. *Bulletin of Syracuse University*, Series IV, No. 1, pp. 14-17, Oct. 1, 1904.

Data on the copulation and eggs.

C. J. H.

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THE BEHAVIOR OF PARAMECIUM. ADDITIONAL FEATURES AND GENERAL RELATIONS.

By H. S. JENNINGS.

Assistant Professor of Zoology in the University of Pennsylvania.

With 17 figures in the text.

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Since *Paramecium* is usually taken as a type for the study of unicellular animals, it is desirable to have its reactions to stimuli as fully known as possible. In attempting to put together the results of numerous investigations made during the last fifteen years on the behavior of this animal, I have found that there are still a number of reactions which have not been described, or have been described incorrectly, and that certain general relations running through the behavior have never been brought out. The present paper attempts to fill, so far as possible, these gaps in our knowledge, supplementing and unifying previous accounts of the behavior of *Paramecium*. The writer tries to point out omissions or errors in his own previous work with the same impartiality as in the works of others.

The chief subjects dealt with are, in the first place, what we may call the *action system* of *Paramecium*; in the second place, the fundamental character of the stimulations to which the animal responds. In the third place an account is given of certain imperfectly or incorrectly known reactions, with particular reference to their relation to the "action system" of *Paramecium*. The chief reactions thus taken up are "rheotaxis," "geotaxis" and "electrotaxis."

Methods.—A word should be said here as to certain methods of work. Throughout the following paper accounts are given of the direction of the *effective* beat of the cilia. This was determined in every case by mingling finely ground India ink with the water containing the *Paramecia*, thus observing the direction of the currents caused by the cilia. By using such a method one is not reduced to conjecture as to the really effective direction of the ciliary beat, as has been the case in certain papers on this subject, but this effective direction is determined immediately by observation. I have supplemented this method by observing the cilia of animals partly confined in a gelatin solution, in the usual way, and of animals partly stupefied with chloretone. These methods gave especially good results when combined with the use of India ink, to show the currents. Owing to its fineness, blackness, and absolute lack of chemical action, I have found the use of India ink (or Chi-

nese ink) much preferable to that of carmine or indigo. The ink is procured in sticks and rubbed up with water in the usual way.

I. THE ACTION SYSTEM.

By the behavior of an organism we mean essentially the regulation, by means of movement, of its relations to environmental conditions. The characteristic complex of movements by which the relations of *Paramecium* to its environment are determined may be called the "action system" of the organism. Most animals have certain peculiar methods of action, depending largely upon their structure—upon what VON UEXKÜLL (1903, p. 269) calls the "biologische Bauplan"—by which most of their behavior is brought about. These characteristic ways of acting are usually few in number and form a unified system, providing a definite reaction combination for any stimulus. The reaction systems of different animals vary as much as do their structures. Thus many different agents acting on a given animal may produce the same set of movements, while on the other hand the same agent acting on organisms of different "action systems" produces in each case different movements. The method of reaction then depends as much on the action system of the organism in question, as upon the physical or chemical action of the stimulus. The usual relation between the two factors may be expressed as follows: The action system supplies a limited number of methods of action, the character of the stimulus (including its localization) determines which of these methods shall be set in operation.

In dealing with the action system of *Paramecium*, we have to consider, first, the usual movements and the environmental relations which they induce; second, the typical modifications of these movements (the reaction types), under the influence of stimulation.

1. *The Usual Movements; Spiral Swimming*.—As is well known, *Paramecium* continually swerves toward the aboral side and revolves on its long axis as it swims through the water, so that its course is a spiral one (Fig. 3). The revolution, so far

as I have observed, is always *over to the left*, when the anterior end is directed away from the observer. That is, the upper surface is continually passing to the observer's left (the lower surface of course to his right).¹ Before using the stereoscopic binocular I supposed that the revolution was sometimes over to the right, sometimes over to the left (JENNINGS, 1899, p. 316). But observation of thousands of cases since this instrument was used has never shown a single exception to the revolution over to the left. I have repeatedly known observers working with the usual monocular microscope to assert that part of the *Paramecia* in a given culture were revolving over to the right, but on examination with the stereoscopic binocular they invariably became convinced that there was no exception to the revolution over to the left. The appearances shown by the monocular microscope are very deceptive in such phenomena, and I do not believe that observations with it even by practiced observers are reliable on this particular point.

The revolution is still over to the left when the animals are swimming backward. This is contrary to the statement made in the second of my "Studies" (JENNINGS, 1899, p. 316), when I was working with the monocular microscope. But the binocular leaves no doubt upon this point. When the forward movement is reversed, the direction of rotation is *not* reversed.

The oral groove of *Paramecium* always passes, if the oral side is down and the anterior end away from the observer, from the right behind to the left in front (as represented in BÜTSCHLI, 1889, Pl. 63, Fig. 1 a). Many observers have reported *Paramecia* in which the direction of the groove is "reversed," running from the middle obliquely to the right instead of to the left.

¹ There is no general agreement as to the designation of the direction of a spiral. The above method seems most convenient for free swimming organisms, since it gives the results of immediate observation, and other methods of designation usually have to be translated, for practical purposes, into this one. If we used the method of designation proposed by NÆGELI (1860), the spiral of *Paramecium* rises from south to west. If we designate the direction of rotation by the method used in spiral cleavage, imagining a small observer situated in the long axis of *Paramecium* with head toward the anterior end (KÖFOID, 1894, p. 180), then we must say that the rotation is to the right.

But the monocular is deceptive on that point. An investigator who was certain that in a particular culture many of the individuals were thus "reversed" made at my request a careful examination of a large number, after killing them with an excellent fixing solution. Not a single reversed specimen was found. If such exist, they are certainly extremely rare.

The obliquity of the oral groove—from right behind to left in front—appears to be the opposite of that which would assist the revolution over to the left. If the groove should act like the groove of a screw, moving along a solid ridge, the animal would revolve over to the right instead of over to the left. It is of course known that the revolution on the long axis is independent of the groove, since when the animal is cut in two in such a way that no part of the groove remains on the posterior half, this half nevertheless continues to revolve on its long axis when moving forward (JENNINGS and JAMIESON, 1902). The significance of the direction of the oral groove is probably to be sought in its relation to the stream of water which it leads to the mouth.

The width of the spiral path of *Paramecium* varies much. The spiral is narrowest when the animal is progressing most rapidly, through water which presents no stimuli; its width is then equal to about one-half the length of the animal. Usually the spiral is wider than this; the length of the animal is perhaps a fair measure of the average width. In many cases, as after stimulation, the width is much greater; it may be several times the length of the animal. *Paramecium* as a rule makes one turn of the spiral, reaching a corresponding phase or position, in about four times its length; but this relation is also variable.

The spiral motion is compounded of three factors: (1) the forward movement; (2) the swerving toward the aboral side; (3) the revolution on the long axis. Each of these factors depends on certain peculiarities in the stroke of the cilia. The forward motion is due of course to the fact that the cilia strike in a general way backward. The revolution on the long axis is due to the fact that the stroke is not directly backward,

but is oblique. This obliqueness in the stroke of the cilia is easily rendered evident by mounting the animals in water containing a large quantity of India ink in suspension, as described above. After the violence of the movement has subsided, specimens may be studied that are restrained by coming in contact with a solid, or by swimming into a crevice. In such specimens, still revolving on the long axis, it may be seen that the particles of India ink on the upper surface of the animal pass backward and, when the anterior end is directed away from the observer, to the observer's right. That is, on the right side of the animal the particles pass toward the oral groove, on the left side away from the oral groove (Fig. 1). This

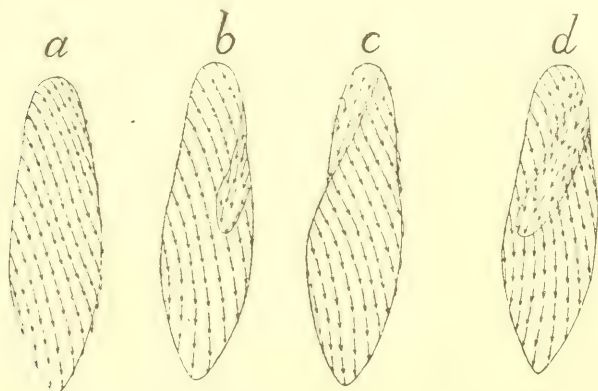


Fig. 1. Diagrams showing the direction of the water currents caused by the cilia, in different positions of the animal. *a*, aboral surface; *b*, right side; *c*, left side; *d*, oral surface.

movement is indicated in a transverse section of the animal by Fig. 6, *a*. It is evident that the ciliary motion thus indicated would turn the animal in the opposite direction from the currents—that is, over to the left. In the oral groove the cilia strike more nearly directly backward, with but a slight obliqueness that is opposite that of the body cilia. This is shown by the fact that a current runs within the groove from its anterior to its posterior end (Fig. 1, *b*, *c*, *d*).

The swerving toward the aboral side is due, in the normal swimming, largely to the more powerful stroke of the cilia in

the oral groove. It may be increased, under stimulation, by a change in the beat of the body cilia of the anterior end at the left side of the oral groove, by which they strike toward the oral groove instead of away from it. On the number and strength of action of the cilia showing the changed beat depends the amount of swerving toward the aboral side.

All the three factors in the spiral course may vary more or less independently of each other, and on the amount of such variations depends the width of the spiral, the number of turns in a given distance, and the like. The effects of stimuli consist largely, as we shall see, in changing the proportional parts played by these various factors—decreasing or stopping one, increasing another, etc.

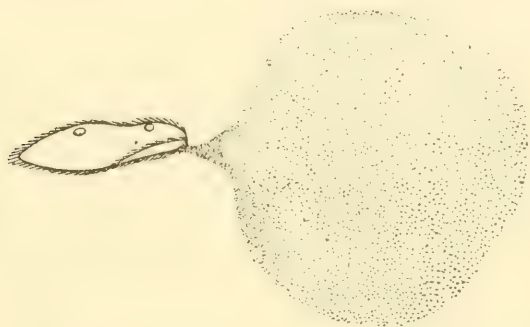
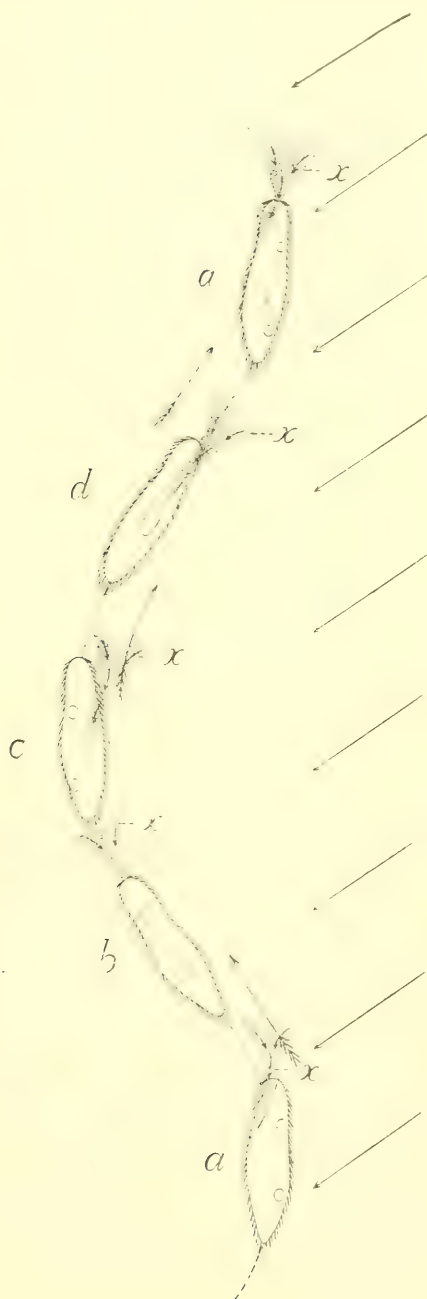


Fig. 2. A *Paramecium* swims toward an area containing India ink; before it reaches the boundary of the area a cone of the ink is drawn out by the action of the oral cilia, reaching the anterior end and oral side.

Owing to the stronger and more direct backward beat of the oral cilia, in swimming forward a current of water is caused to pass from in front in the form of a cone to the oral side and mouth. This is rendered evident when a cloud of India ink is added to the water containing many *Paramecia*. The cloud has for a time a definite boundary surface. When the *Paramecia* swim toward this surface, the latter may be seen to extend out in the form of a cone, to meet the advancing animal (*Fig. 2*). As soon as this black cone comes in contact with the anterior end of the *Paramecium*, the latter stops and turns in another direction—this occurring some distance from the gen-



eral boundary surface of the cloud. This explains the observation often made that *Paramecia* and other infusoria react and turn away seemingly some distance before reaching the agent causing the reaction. Thus, on approaching a bubble or the free surface of the water, infusoria often react and turn away when still separated by a marked interval from the air surface. A little of the water next to the air has been drawn out to meet the animal, which then reacts to any modification the water may have undergone by contact with the air.

Thus in its forward course the animal is continually receiving "samples"

Fig. 3. Spiral course of *Paramecium*, showing how the animal is subjected through this method of swimming to many changes in its relation to the environment. The arrows at the right indicate some agent (light, gravitation, a water current or the like) acting from a definite direction: the relation of the animal to this agent is continually changing; at *b* the body is nearly transverse, at *d* nearly parallel to the arrows. The dotted areas *x* show the currents of water carried to the anterior end by the movements of the oral cilia.

of the water in front of it, and reacting to these samples. In its spiral path *Paramecium* becomes pointed successively in many different directions, so that it "samples" the water from many directions (Fig. 3). When the spiral is very narrow, the animal swimming rapidly forward, these samples all come from near the axis of the spiral and therefore show little variation. But in most cases the direction from which they come is continually changing. Thus we may say that *Paramecium*, through its spiral course, is continually "trying" the water in various directions. Or, to express the same thing in a more objective way, through the spiral course the most sensitive portion of the organism is subjected successively to water coming from many different regions.

In another way the spiral course subjects the organism to varied experiences. Suppose that a force which acts in straight lines from a definite direction is operating on the swimming organism from one side; for example, light, or the electric current, or gravity, or a current of water. By its spiral course the organism is brought successively into different relations with this agent (Fig. 3). In one phase of the spiral, as at *d*, it swings more nearly into parallelism with the lines of action of the agent; in another it is becoming more nearly transverse, as at *b*. In the case of light the anterior end is becoming more illuminated in one phase, less in another; in other words, the anterior end is subjected to continual variations in the intensity of illumination. With gravity, or a water current, the swinging is assisted in one phase of the spiral, resisted in another, so that the animal is subjected to continual variations in the resistance it meets. These changes give opportunity for directive or regulative stimulation. It is only when the axis of the spiral course is in the lines of force—in other words, when the organism is "oriented"—that such changes cease. These relations will be brought out in detail later in describing the reactions to certain stimuli.

Altogether, we see that the "action system" of *Paramecium* contains elements of such a nature as to subject the animal to the greatest possible number of changes in the environment, thus giving it opportunity to react to all such changes.

2. *Modification of the Movements under Stimulation; Reaction Types.*—In the behavior of *Paramecium* under the action of stimuli we may recognize a certain number of distinct reaction types. (1) The chief one of these is that which I have in former papers called the "motor reflex" or "motor reaction," and which I shall call here, for reasons given later, the "avoiding reaction." The others are (2) the movement forward from the resting condition; (3) the coming to rest of a moving individual; (4) certain features of the reaction to the electric current; (5) local contractions of the body, and possibly (6) the discharge of trichocysts. The list of reaction types thus rises to a considerable number, but the last three named play almost no part in the regulation of the relations of *Paramecium* to its environment under natural conditions. We shall deal *in extenso* here only with the most important reaction type—the "avoiding reaction."

3. *The Avoiding Reaction.*—Through this reaction type occur most of the marked reactions of *Paramecium* that have often been spoken of as "tropisms" or "taxes;" in other words, the reactions to stronger stimuli of all sorts. The avoiding reaction consists, when well marked, of the following: the animal swims backward, turns toward the aboral side, then resumes the forward motion. I have called this in former papers the "motor reaction" or the "motor reflex." But the former is a general term, properly used for any movement that takes place as a response to a stimulus, and hence not fitted for characterizing a special reaction type. To the second, objection has been raised on the ground that the word *reflex* should be used only when a nerve cell is concerned; there are perhaps other and better grounds for leaving open the question whether the movement in this reaction is in the nature of a reflex or not. For these reasons I have sought for a simple expression which shall bring out the essential character of the reaction without prejudice to its nature in other respects. The most general effect of this reaction is to remove the reacting organism from the source of stimulation and direct it elsewhere; it may, therefore, be appropriately called the "avoiding reaction." By this reaction,

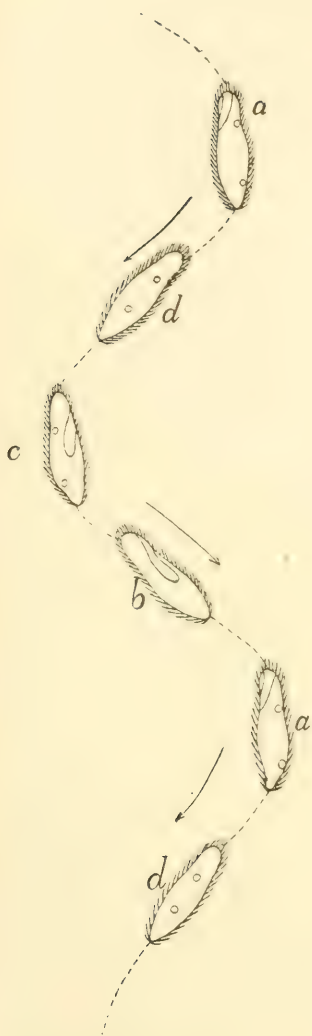


Fig. 4. Backward spiral course of *Paramecium* in reacting to a stimulus. *d, c, b, a*, successive positions occupied. The turning is to the left, in the same direction as in *Fig. 3*.

as I have shown in previous papers, *Paramecium* responds to heat, cold, mechanical stimuli, chemicals of all sorts, osmotic stimuli—in fact, to stronger stimuli of almost all classes.

The avoiding reaction is brought about through certain modifications of the three factors in the spiral swimming. The first phase of the reaction is a slowing, suspension or reversal of the forward component in the spiral course. In a very pronounced reaction, caused by a powerful stimulus, the forward course is reversed, while the revolution on the long axis and the swerving toward the aboral side continue as before. The animal therefore swims spirally backward for a distance (*Fig. 4*). When the stimulus is weaker, the forward course is merely suspended for a moment—the revolution and swerving toward the aboral side continuing. Finally, in some cases the forward course is merely made slower. The backward swimming or stoppage is brought about by a reversal of the forward component in the stroke of the cilia. In

a pronounced reaction all the cilia are reversed (*Fig. 4*); in a less marked reaction the body cilia are reversed while the oral cilia are not (*Fig. 5*). In the latter case the effect on the currents in the water, as shown by the movements of particles of India ink, is

peculiar. The currents pass forward everywhere, save in the oral groove, where they pass backward. Since the animal at the same time revolves on its long axis, the particles in a given region close to the Paramecium at first dart forward, then later backward, depending on whether the body surface or the oral groove is directed toward the region in question.



Fig. 5. Currents in the reaction to a weak stimulus, or near the end of a reaction to a strong stimulus. The animal moves backward: the body cilia are reversed, the oral cilia are not. The arrows show the direction of the water currents.

from the oral groove (Fig. 1, *c*). But in the avoiding reaction, both while the swimming backward continues and after it has ceased, the cilia of both right and left sides strike toward the oral side. This of course drives the body of the animal toward the aboral side. The difference between the stroke of the cilia in the usual course, and in the avoiding reaction is shown in sectional views in Fig. 6.

Thus the cilia to the left of the oral groove play a most important part in the avoiding reaction, reacting by a reversal of the direction of the usual stroke—at least by a reversal of

The second feature in the avoiding reaction is the increased turning toward the aboral side. This is due to two changes in the stroke of the cilia. The first and less important is the fact, mentioned above, that after a stimulus of not very great intensity the body cilia are reversed, while the oral cilia continue to beat backward. This of necessity turns the anterior end toward the aboral side. The second and more important factor is a change in the stroke in the body cilia of the left side, in the anterior portion of the animal. In the ordinary swimming, as we have seen, the cilia of the right side strike toward the oral groove (Fig. 1, *b*), those of the left side away

the transverse or oblique component of the stroke. They thus play a part similar to the large cilia at the left of the peristome in the *Hypotricha*, and to the cilia which WALLENGREN (1902) designates as the "*Drehungswimpern*" in *Opalina*. It is to their reversal that the most characteristic features of the reaction are due.

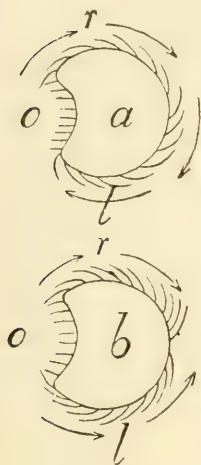


Fig. 6. Diagram of cross sections of *Paramecium* (viewed from the anterior end), showing the obliquity of the ciliary stroke. *a*, condition in the usual forward progression: the body cilia all strike toward the right side; *b*, condition while turning toward the aboral side, in reacting to a stimulus: the cilia of the left side have changed the direction of their stroke; *l*, left side; *r*, right side; *o*, oral groove. The arrows show the direction in which the cilia tend to turn the body.

avoiding reaction the cilia of the left side tend to turn the body to the right, those of the right side to turn it to the left (Fig. 6, *b*). Thus the cilia of the two sides oppose each other so far as revolution is concerned, but co-operate in causing the body to swerve toward the aboral side.

The effectiveness of the change of beat of the cilia of the left side varies much, apparently as a result of the fact that the number of cilia having the changed stroke varies. On this point it is exceedingly difficult to determine numerical or precise quantitative relations. But if the stimulus is weak, appar-

ently only a few of the cilia at the anterior tip of the left side change their direction of stroke; with a stronger stimulus the number is greater. It is possible further that the amount of change in the stroke of individual cilia is variable; from some of my observations I believe this probable. But whatever the nature of the variation, the following results are produced. If the effective beat of these left cilia is only slightly changed, the anterior end then describes but a small circle, as in Fig. 8, *a*. As the effective beat of these cilia changes farther, the swerving becomes stronger and the revolution slower, so that the anterior end swings in a larger circle (Fig. 8, *b*). Finally all the cilia beat toward the oral side; the revolution on the long axis has then entirely ceased, while the swerving toward the aboral side is very rapid. As a result the anterior end describes the circumference of a circle, in the radii of which lies the long axis of the body (Fig. 9). Thus the swerving toward the aboral side varies inversely as the rate of revolution on the long axis. In the unstimulated swimming the revolution is rapid and the swerving slight; in the strongest reaction the revolution is zero and the swerving is strong, while between these two extremes an indefinite number of gradations exist. The change in the forward stroke of the cilia seems more nearly independent of the two interconnected sets of changes just described. The rapid forward swimming may be combined with the minimum of swerving and the maximum of rotation; the animal then shoots rapidly forward. On the other hand, the forward swimming may either entirely cease, or be converted into a backward movement, in combination with the same minimum of swerving and maximum of rotation. In the former case the animal merely rotates rapidly on its long axis, neither advancing nor retrograding; in the latter case it shoots rapidly backward. But whenever the swerving toward the aboral side becomes largely increased, the longitudinal motion seems to decrease; this is probably a necessary consequence of the fact that the effective stroke of many of the cilia is in this case lateral, so that only a comparatively weak component is left for movement along the long axis. While swerving strongly, how-

ever, the longitudinal motion may be either forward, or zero, or backward.

As our analysis thus far shows, it is quite inadequate to conceive the cilia as having merely forward and backward strokes—"expansive" and "contractile" phases. The effective stroke may be nearly straight backward or forward; or obliquely backward or forward, with various grades of obliqueness; or transverse. Furthermore, the cilia of different parts of the body may vary independently in their effective stroke. Thus, we have above distinguished the following conditions:

1. All the cilia strike almost directly backward (forward course, Fig. 3).
2. All the cilia strike almost directly forward (backward course, Fig. 4).
3. All the cilia strike obliquely backward and to the right, save the oral cilia, which strike nearly directly backward (forward course, with much swerving toward aboral side).
4. All the cilia strike obliquely forward and to the right, save the oral cilia, which strike nearly directly forward (backward course with much swerving).
5. All the cilia strike transversely to the right (rotation on the long axis, without progression or retrogression.)
6. The cilia of the right side strike obliquely to the right and backward; the cilia of the left side strike obliquely to the left and backward (forward course, swerving to the aboral side, without rotation).
7. The cilia of the right side strike obliquely to the right and forward; the cilia of the the left side strike obliquely to the left and forward (backward course, swerving to the aboral side).
8. All cilia strike obliquely forward, save those in the oral groove, which strike backward (backward course after a weak stimulus, or after the effect of a strong stimulus has nearly expired, Fig. 5).

It must be added that the extent of body surface on which the cilia show any of the characteristic strokes mentioned is exceedingly variable. Often, for example, the body cilia of only the anterior tip or the anterior half, show the transverse stroke, while posterior to this they do not. Farther, the cilia of the posterior half of the body frequently cease beating effectively, showing only a slight quivering, while the anterior cilia are still very active. As a result of a long study of the ciliary movements, one retains the impression that almost any combination of forward, reversed, oblique or transverse strokes is possible among the different areas of the body, and that those mentioned above are only typical combinations, produced under more or less definite conditions. As a rule a combination is produced such as brings about a well ordered movement of some sort, but under certain conditions the movements of the cilia are such as to produce only a disordered quivering or jerking, without movement in any definite direction. This is sometimes the case for example when the animal is immersed in a strong chemical. Under some conditions a similar result is produced also, as we shall see later, by the electric current.

What are the conditions on which depends the direction of the effective stroke of the cilia in any given region of the body? The question is a very difficult one. According to the tropism theory, the direction of the effective stroke of the cilia—that is, whether the “contraction phase” or “expansion phase” was the effective one in producing movement—depended on the direct action of stimuli on the part of the body bearing the cilia in question. Certain agents impinging on any given region of the body caused the “contraction” or backward stroke to be more effective; others had the opposite effect. But we now know that this conception was far too schematic. As a result of a stimulus applied to a single definite region of the body, certain cilia beat effectively in one way, others in a different manner, and the first effect is soon followed by a second one, equally complicated. Thus, a touch at the anterior end with a glass rod, or a chemical acting on the surface, (1) produces reversal of the stroke of the cilia over the entire body; (2) then

a return of the oral cilia to the backward stroke, the others remaining reversed; (3) then causes the body cilia of the left side to strike toward the oral groove (whereas before they struck in the opposite direction), while the forward stroke of the body cilia becomes converted into a backward one. There is a co-ordinated system of movements, producible in many ways, a system that is variable in many respects, yet as a rule varies in such a way as to retain throughout its co-ordination.

The change in the stroke of the cilia is correlated in many cases with certain other phenomena. *Paramecium* still retains to a very slight degree the power of contraction that is so marked in many other ciliates. The anterior end especially

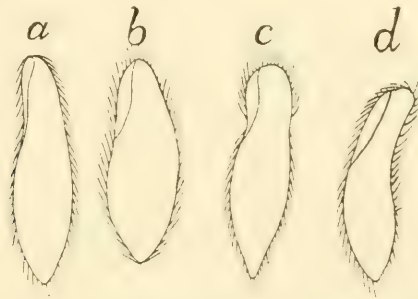


Fig. 7. Relation of reversal of the ciliary stroke to contraction. *a*, usual condition: over the entire surface of the slender body the cilia strike backward; *b*, the body is contracted, becoming short and thick: all the cilia are reversed; *c*, anterior end alone contracted, and cilia reversed in this region alone; *d*, contraction on the aboral side, curving the body: cilia reversed in the contracted region.

may be shortened and thickened, or narrowed and lengthened, or bent to one side, to an appreciable degree. These movements are hardly to be observed in specimens swimming freely through the water. But if the movements are impeded and the animals partly flattened out between the slide and cover, partial contractions are very evident. It is then to be observed that whenever contraction takes place, the cilia of the contracted region become partly or entirely reversed (*Fig. 7, b*), beating no longer forward, but backward or transversely. At times the whole body contracts, becoming shorter and thicker; at the

same time it begins to swim backward. The moment the more slender form is restored, the animal begins to swim forward. Frequently only the anterior half or anterior tip is contracted (Fig. 7, *c*); then the cilia are reversed in this region alone. Again, one often sees the aboral side contract strongly, so that the animal curves toward this side. At the same time the cilia are reversed on this side, while they continue to strike as usual on the oral side; the animal then of course turns toward the aboral side (Fig. 7, *d*). Is this coincidence of the reversal of ciliary movement with contraction to be considered a necessary relation, so that whenever contraction occurs, the cilia must be reversed? STATKEWITSCH (1903) shows that the same relation exists in the reaction to induction shocks, so that the generalization seems very probable.

4. *The Avoiding Reaction as a Factor in Behavior.*—

Let us now leave the detailed physiology of the avoiding reaction, and consider it as a factor in behavior; that is, its effect on the relation of *Paramecium* to the environment. We may, for the sake of a vivid realization, put the conditions in the form of a problem, with a slightly subjective tinge. The *Paramecium* has been swimming forward without stimulation; on reaching a certain region it is stimulated. What is to be done in order to avoid or escape the stimulation?

The first feature of the reaction—the swimming backward or stopping—of course either removes the animal from the region where it is stimulated, or prevents it from entering farther. This reaction is, logically if we may so express it, an absolutely correct one. Since the animal was not stimulated till a certain point is reached, then *was* stimulated, in order to avoid the stimulation it is sound practice to retrace the course; in other words, to restore the condition which did not stimulate. With the swimming backward the direction of the water currents is likewise reversed, so that no more of the water from the stimulating region is brought to the mouth.

The next problem is, in what direction shall the *Paramecium* now swim forward so as to avoid further stimulation? To determine this, it would be well if a trial could be made of the

different conditions immediately in advance. This is exactly what the Paramecium does. It begins to turn toward the aboral side, at the same time continuing to revolve slowly on the long axis. In this way the anterior end swings about in a circle and is pointed successively in many different directions (Fig. 8). From each direction a little water is brought to the anterior end and mouth by the oral cilia. Thus the Paramecium is given opportunity to "try" the water in many different directions. When the water coming from a certain one of these directions does not show the conditions which acted as a stimulus, the ani-

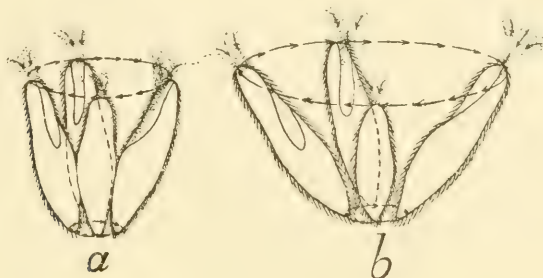


Fig. 8. Diagrams of the way in which Paramecium swings its anterior end about in a circle, in reacting to stimuli. *a*, reaction to weak stimulus; *b*, reaction to a stronger stimulus. From each different direction a current of water is brought to the anterior end. (The forward or backward component of the motion is omitted from the diagram).

mal may move forward in that direction, since now there is no further cause for reaction. If the original stimulus was weak, the anterior end is swung about in a small circle, "trying" the water from a number of directions varying only a little from the original one (Fig. 8, *a*). If the stimulus was very strong, after swimming backward a long distance the animal swings its anterior end about a larger circle, a circle of which the longitudinal axis forms one of the radii; thus directions are "tried" which diverge as much as possible from the original one (Fig. 9). If in any of these "trials" the stimulus is again strongly received, the animal may repeat the whole reaction from the beginning—retracing its course anew, and beginning a new set of "trials."

With a very powerful stimulus, such as a strong chemical, this reaction makes the impression of being violent and disordered, as indeed may the reactions of a human being under similar conditions. But with a moderate stimulus the reaction may be very delicate. This may be illustrated by the behavior of *Paramecia* within an area of water containing carbon dioxide. Part of the reaction under these conditions was described

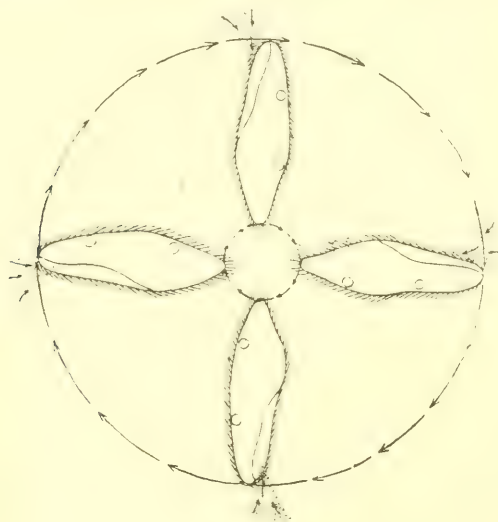


Fig. 9. Diagram of the swinging of the anterior end about a large circle, in reacting to a strong stimulus. The revolution on the long axis has entirely ceased.

in one of my earlier paper (JENNINGS, 1899, p. 331), though without a full appreciation of its real significance. The *Paramecium*, swimming slowly within the area of carbon dioxide, comes near to the edge of the area, where it receives water containing none of the gas in solution. This change acts as a very mild stimulus; the organism merely stops and swings its anterior end gently toward the aboral side, "trying" a new direction. If the water now received is still without the carbon dioxide, the *Paramecium* swings its anterior end still farther, at the same time continuing to revolve on the long axis, which changes the direction of swinging. As soon as the water it receives contains carbon dioxide, it swims ahead, changing its

course only when it again receives water without the gas in solution. The reaction under such conditions is a very delicate one, keeping the animal in close touch with the environmental conditions. The behavior does not impress one as a definite "reflex"; the Paramecium is seen merely to change its course a little after trying several slightly differing directions.

The behavior of Paramecium in swinging its anterior end about in a circle is essentially similar to the "feeling about," "searching," or "trial" of a higher organism. We know, of course, no more of subjective qualities in any organism outside the self than we do in Paramecium. If we describe the "feeling about" or "searching" of any higher animal in a purely objective way, we shall find that the description takes essentially the same form as for Paramecium. Under certain conditions the organism performs certain movements, which subject it to certain environmental changes. As long as the conditions remain of essentially the same character, it continues these movements. As soon as these movements induce conditions differing in a certain way, the movements stop. This description fits equally well the movements of a cat trying to escape from a cage (see THORNDIKE, 1898), of a dog searching for a bone, and of Paramecium reacting to carbon dioxide. In its method the behavior seems fundamentally similar throughout.

The behavior of Paramecia under such "repellent" stimuli follows then, perhaps, as effective a general formula as could be devised. When stimulated it performs movements which take it away from the source of stimulus, and direct it successively in many ways, until the stimulation ceases. Reaction of this character is essentially that of "trial and error" as we find it in higher animals. From this standpoint the behavior may be summed up as follows: When there is "error" the organism "tries" various directions or methods of action till one is found in which the "error" ceases. These relations have been brought out by the author for lower organisms in general in a previous paper (JENNINGS, 1904, *b*).

We must ask here the question whether the reaction method of Paramecium above described should or should not

be called a *reflex*—a term which I have applied to it in previous papers. The question which interests us here is not whether an act performed without the intervention of a nervous system may properly be called a reflex; it may be strongly doubted whether the anatomical structure of organisms forms a proper basis for classification of types of behavior. But does the reaction method described fall in the concept of a reflex, judged merely as a type of behavior?

A reflex is commonly described as a fixed and invariable method of response to a definite stimulus. It is rare, however, that such definitions are found to be rigidly maintainable for given instances; the excellent discussion of HOBHOUSE (1901) shows how the reflex concept must be modified and its limits effaced, till it flows easily into other behavior types, before it can be applied to the phenomena actually found in animal behavior. Such a process of softening down is certainly necessary before we can make the reflex concept apply to the avoiding reaction of *Paramecium*. This reaction is composed of three factors, which may vary more or less independently of one another, in such a way that an absolutely unlimited number of combinations may result, all fitting the common reaction type. The possible variations may be expressed as follows: If the *Paramecium* be taken as a center about which a sphere is described, with a radius several times the length of the animal, then as a result of the avoiding reaction the *Paramecium* may traverse the peripheral surface of this sphere at *any point*, moving at the time either backward or forward. In other words, the reaction may carry it in any one of the unlimited number of directions leading from its position as a center. While the direction of turning is absolutely defined by the structure of the animal, yet the combination of this turning with the revolution on the long axis permits the animal to reach any conceivable position with relation to the environment. In other words, *Paramecium*, in spite of its curious limitations as to method of movement, is as free to vary its relations to the environment in response to a stimulus as an organism of its form and structure *could* conceivably be.

Again, the reaction at times keeps the organism in the closest possible touch with the environment, continuing as long as certain conditions continue, increasing in effectiveness as the conditions causing it increase in intensity, and ceasing when the conditions causing it cease, maintaining the organism throughout in certain relations with the source of stimulation. Altogether, I believe that the following admission must be made. If we consider the reaction of *Paramecium* a reflex, it is because we are convinced beforehand that such an organism *can* show only reflexes. If the actions of *Paramecium* did belong to some higher type of behavior, there could be little objective evidence of this, beyond what we already have.

In *Paramecium* the reaction has not been shown to be modifiable by previous experience, so that from this criterion the behavior retains the characteristics of a reflex. But in a close relative, *Stentor*, such modification by experience has been demonstrated (JENNINGS, 1902), so that it may be presumed that technical difficulties alone have thus far prevented our observing it in *Paramecium*.

The effectiveness of the method of reacting by "trial and error" that we have described above for *Paramecium* depends upon the power of discrimination of the reacting organism. By "discrimination" of stimuli we mean, in an objective study of behavior, that the organism reacts differently to the different stimuli in question. In this sense *Paramecium* discriminates acids from alkalies and salts, and these again from sugar. Furthermore, it discriminates different strengths of solution, reacting differently, for example, with relation to weak and to strong acids. On the other hand, it does not effectively discriminate different acid substances, save in so far as one is stronger than another. Thus it swims into weak carbonic acid, which is harmless, and likewise into weak sulphuric acid and copper sulphate, which kill it. It does not markedly discriminate a ten per cent sugar solution from water, hence it swims readily into such a sugar solution and is killed by the osmotic action.¹ Thus in re-

¹ Details as to the facts cited are given in my previous papers on *Paramecium* here we are concerned only with the interpretation of these facts.

gard to powerful acid substances and to sugar solution it makes what we would call in ourselves a "mistake." In higher animals we recognize that the power of accurate discrimination is one of the "higher" powers, becoming more secure as development progresses. We cannot, therefore, be surprised that it should not be perfect in so low an organism, nor that such organisms, through lack of discrimination of injurious and non-injurious agents, often react in a way that leads to their destruction. Any organism reacting by the method of "trial and error" is subject to the possibility of destruction in some of the "trials."

This method of "trial and error," based on the "avoiding reaction" above described, plays a large part in the behavior of *Paramecium*. Through it are produced the "negative" reactions to agents of all sorts, as well as the collections formed in certain chemicals, in regions of optimum temperature, and the like. On the other hand, there exist certain reactions in which the final relation to the environment is brought about in a more direct way—notably "positive thigmotaxis" and certain features of the reaction to the electric current. These reactions will be taken up later.

II. NATURE OF STIMULATION.

Just what is the nature of the stimulation which produces this reaction by "trial and error" in *Paramecium*? An examination of the facts shows that as a general rule the effective stimuli consist of some *change* in the conditions, or, what is the same thing to the organism, of some change in the relation of the organism to the conditions. Change is the essential feature in producing the chief reactions of *Paramecium*.

This statement requires of course some qualification in detail. A change may be nearly instantaneous, while the consequent reaction of the animal of course requires time, and must, therefore, continue for a certain period after the change has been completed. If the animal is suddenly subjected to a one-fourth per cent solution of common salt, it continues to react for a short time after the instant of the change, though if the

conditions now remain constant, it soon ceases to react. The length of time the reaction may continue after the change is completed varies with different agents, becoming longer as the agent is more powerful. The phenomena may be expressed in the following somewhat indefinite way: the animal reacts to the change as long as *its effect as a change* continues. In the limiting case of a stimulus so powerful as to be destructive, the reaction may continue for a considerable period, till death intervenes. In such cases we have then a continued reaction to a condition that remains constant for some time. But with destructive agents, the action of the agent seems progressive, so that there is really a continual change in the relation of the organism to the agent, till the progressive series of changes ends in death. Whatever the explanation in these rare cases of destructive conditions, change is elsewhere the fundamental feature of the stimuli producing the chief reactions in *Paramecium*. This is the result which stands out clearly from all my work on stimulation in *Paramecium*.

A change from one condition to another produces a reaction when neither the preceding nor the following condition, acting continuously, produces any such effect. Thus, *Paramecia* may live and behave normally in water at 20° or at 30°, yet a change from one to the other, or a very much less marked change, produces the avoiding reaction. *Paramecia* may live without reaction in tap water or in water containing one-tenth per cent sodium chloride, but the change from the former to the latter produces the avoiding reaction. This relation could be illustrated by innumerable cases, taken from my earlier papers on *Paramecium*.

In all cases of course a *certain amount* of change is required in order to produce reaction; in other words, there is a certain necessary threshold of stimulation. Since the change itself is the real cause of the reaction, it is probable that the amount of change necessary will bear some definite relation to the intensity of action of the agent in question before the change. In other words, it is probable that the reactions are subject to WEBER's law, as they are known to be in bacteria (PFEFFER,

1904, p. 625). The corresponding quantitative relations have not been worked out for *Paramecium*.

The fact that change is the essential feature in causing reaction is of course correlated with the fact that organisms become acclimatized, so far as reaction is concerned, to a certain strength of stimulus. To say that the organism becomes thus acclimatized is indeed little more than to say that it reacts only to changes.

The change which produces stimulation may be a direct alteration in the environment, as when a chemical is brought near a specimen, or when it is touched at the anterior end with a glass rod, or when the temperature is raised or lowered from without. But under natural conditions the change is more usually produced by the movements of the animal itself. In its rapid swimming the animal passes from one region to another, the conditions in one region changing to those in the next, and thus causing reaction. Further, as we have seen, the spiral course gives opportunity for frequent changes to act upon the organism; the anterior end is pointed successively in many directions, receiving "samples" of water from each direction. The greater the swerving in the spiral course the greater the opportunity for frequent changes to affect the animal. The avoiding reaction, with its swerving in many directions, may indeed be looked upon as a method of subjecting the organism successively to many changes.

It is, however, not mere change *per se* that causes the reaction, but change of a certain kind or in a certain direction. Of two opposite changes, one usually produces the reaction, while the other does not. *Paramecium* reacts when it passes out of a weak acid, not when it passes in; it reacts when it passes into an alkali, not when it passes out. A *Paramecium* at 28° reacts at passing to a higher temperature, not at passing to a lower one; a *Paramecium* at 20° shows the opposite relations. The direction of change which produces the avoiding reaction may be briefly characterized as that leading *away from the optimum*, while change leading toward the optimum produces none. It is thus clear that in most cases the actual determining factor

in the reactions is the direction of movement of the animal, not the mere orientation, as has sometimes been held. The significance of these relations in connection with the theory of general "pain reactions" I have considered elsewhere (JENNINGS, 1904, *b*). Here we may point out, as a relation of some interest, that in *Paramecium* it is an injurious or negative stimulus that primarily induces motor reactions. This is not at all in agreement with the theory sometimes set forth, that the effect of such stimuli is to cause a cessation of activity.

In no case, so far as I am aware, has it been shown that the reaction in *Paramecium* is due to the difference in intensity of a graduated stimulus on the two sides or ends of the animal, as is assumed by the orthodox tropism theory. In most cases it has been demonstrated that the determining features of the reaction are not of this character.

I have above illustrated the fact that in reactions to chemicals and in temperature reactions, it is a change that causes the response; details are given in my previous papers. In the reactions to changes in osmotic pressure, a very marked change to a higher pressure is required to produce reaction; the opposite change, even to distilled water, is without effect. In the reaction to mechanical stimulation, sudden contact of the anterior end with a solid produces the reaction, though continuous contact is of no effect. *Paramecium* is not, so far as known, sensitive to light. But in other infusoria the writer has recently shown (JENNINGS, 1904) that it is the change in light intensity, at the sensitive anterior end, that induces reaction. The reaction occurs when the change is due to an actual alteration in the source of light, or when it is due to a movement of the organism. Orientation is produced through the fact that in the spiral course the anterior end of an unoriented organism is repeatedly subjected to changes in illumination. To these changes it reacts, by the method of "trial and error," above described, till it comes into a position where such changes no longer occur; such a position is found only when the animal is oriented. The reactions to light are particularly instructive for the part played by the spiral course, with its swerving from side to side, in

causing changes in the intensity of the stimulus, and hence in determining the reactions. While in *Paramecium* there is no reaction to light, certain other reactions are produced in the manner just set forth. These reactions we shall analyse in the next section of this paper.

III. REACTIONS TO CERTAIN STIMULI, WITH SPECIAL REFERENCE TO THE PART PLAYED BY THE "ACTION SYSTEM."

A. Reactions Produced through the "Avoiding Reaction."

1. *Reactions to Water Currents ; Rheotaxis.*—Under rheotaxis is usually understood the orientation of the organism in line with a water current, and movement with or against the current. I have come across a reference to such a reaction to water currents in *Paramecium* only in two papers dealing primarily with reactions to the electric current—namely the papers of DALE (1901) and STATKEWITSCH (1903, *a*). DALE says: "It is sufficient to watch the behavior of *Paramecium* in water contained in a tall jar in which convection currents have been produced, in order to be convinced of its tendency to swim with a stream of water" (DALE, *l. c.*, p. 354). He attempts to use this tendency to swim with the current in explaining the movement to the cathode in the reaction to electricity, but has no farther observations on rheotaxis itself. STATKEWITSCH (1903, *a*, pp. 102-104) likewise observed that *Paramecia* swim with currents caused by the absorption of water by porous substances, but showed that this has nothing to do with the movement to the cathode, since the latter occurs in the same way, whatever the direction of the water currents.

I have carefully examined the reaction of *Paramecium* to water currents under various conditions. The reaction varies with different individuals, and it is difficult to arrange the conditions in such a way as to make the reaction a very precise one. But in all my experiments a large majority of the animals showed the opposite relation to the direction of the current from that mentioned by DALE and STATKEWITSCH. They turned the anterior end up stream and moved against the current. There were usually a number of individuals, however, that

showed the opposite relation, and I can well believe that in some cultures the majority may conduct themselves in this manner, and that this was the case with the *Paramecia* observed by the authors named. But certainly as a rule most of the organisms swim against the current, not with it. The phenomena may best be observed by placing *Paramecia* in a tube which is narrowed in the middle and open at both ends. Only the central part of the tube is filled with water, the two ends containing only air. Over the two ends are fitted rubber caps, such as are used for medicine droppers (Fig. 10). By compressing



Fig. 10. Tube for study of the reaction to water currents. See text.

one of these caps the water is forced through the narrow part of the tube with any desired velocity, and is always under complete control. With a certain velocity of current most of the animals are seen to become oriented and to swim against the current. The tube must not be too narrow, since in this case many of the individuals strike against the side of the tube, and then no longer respond well to the current, the contact reaction interfering with "rheotaxis" as well as with many other reactions. In any case, many individuals show no orientation or are oriented in the opposite direction, yet the phenomenon is sufficiently general to show clearly that we have here a real reaction of the organism.

How is this reaction to water currents brought about? If we direct a fine current of water for a moment upon a *Paramecium* that is swimming quietly, we find that it gives the "avoiding reaction" in a not very pronounced form. That is, it stops, or begins to progress more slowly, and swerves more strongly toward the aboral side, appearing thus to swing from side to side, the anterior end really describing circles of considerable size, as in Fig. 8, *b*. The effect of this current on the animal is of course to change in some way the resistance it

meets in swimming, or the pressure of the water upon it. Such an environmental change produces, then, like many other changes, the avoiding reaction, with its "trial" of different directions. The same result is produced by setting the water in motion in other ways, as by causing the vessel containing the animals to vibrate back and forth.

If now we produce a more extensive current, and allow it to continue, as in the experiment shown in Fig. 10, we find the same result produced. The animals at first pause, then swing the anterior end about in a circle, thus "trying" many different directions. They then swim forward in one of these directions. The reaction is then repeated, and this occurs as a rule several times, until they have come into a position with anterior end directed up the stream. The reaction then ceases; the animals swim forward in the usual spiral manner. They have become oriented by the method of "trial and error," the "trials" continuing till the position of orientation was reached.

We have seen that the original cause of the reaction was a change in the environment—the movement of the water—causing a change in the resistance or pressure the *Paramecium* meets. But why does the reaction continue till orientation is reached, then cease? Consideration of the relation of the current to the spiral course followed by the animal shows that this is exactly what we should expect from all that we know of the behavior of the animal and the cause of the present reaction. Consider a specimen that is swimming transversely or obliquely to the current, as in Fig. 11. In its spiral course it swings the anterior end first against the current, to the point *a*, then with the current to the point *b*. In the swing toward *a* the movement is resisted by the current; in the swing toward *b* it is aided by the current.¹ Its relation to the current thus changes during each turn of the spiral; in one phase the movement is "easier" from being aided, in the next more difficult, from be-

¹ The upward and downward movement of the swing may be neglected for our present purpose.

ing resisted. As we know, exactly such changes act as stimuli, and the animal reacts, as we have seen, in the usual way. It swings its anterior end about in a circle, so that the body axis occupies successively many positions, and continues or repeats this reaction as long as it is subjected to the changes mentioned. But when it comes into a position such that its relation to the current remains constant, it no longer reacts, for to constant conditions, unless destructive, *Paramecium* soon becomes acclimatized. Such a position is found only when the axis of the spiral path coincides with the direction of the cur-

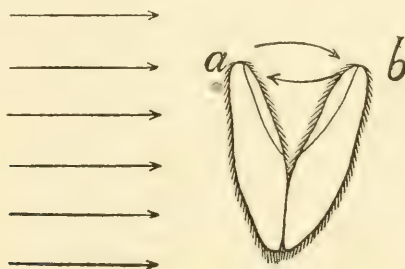


Fig. 11. Diagram to illustrate the cause of the reaction to currents of water. The straight arrows indicate the direction of the current. The swinging of the unoriented *Paramecium* in its spiral course from the position *b* to *a* is resisted by the current, while the movement from *a* to *b* is assisted. (The same diagram illustrates the conditions in the reaction of gravity, if the straight arrows represent the direction of gravity).

rent. In this position the animal of course still swims in a spiral, the anterior end describing circles about the axis of the spiral. But in every phase of the path the axis of the body forms the same angle with the axis of the spiral, and hence with the direction of the water current, so that its relation to the current remains constant, and there is no farther cause for reaction. Orientation has been attained through the "method of trial and error."

But why do the majority of the animals become oriented with anterior ends against the current? Our description thus far accounts for the position of the body axis, but not for the more usual direction of the anterior end. We know that as a rule when *Paramecium* is subjected to changes of opposite char-

acter, such as may be called plus and minus, it reacts to one of these changes, but not to the opposite one (above, p. 466). In its spiral course the unoriented organism is subjected, under the action of a water current, to plus and minus changes in resistance. As a rule it is the minus change that induces the reaction, while the plus does not. This is perhaps intelligible, from the fact that *Paramecium* normally receives some resistance in its swinging toward the aboral side, so that when the pressure of the current comes from the oral side, *driving* the animal toward the aboral side, the change from the usual condition is a very marked one. Therefore, whenever the *Paramecium* swings from *a* to *b*, Fig. 11, a reaction is induced, causing strong swerving toward the aboral side. This is effective in the next phase of the spiral, causing the animal to swing far in the direction $b \rightarrow a$ (since the aboral side is now toward *a*); thus the animal becomes more nearly oriented. Since this movement from *b* to *a* involves only a plus change, it causes no reaction; the ordinary spiral swimming is resumed, so that in the next phase the animal swerves only a short distance toward *b*. But this involves the minus change, inducing reaction again; so in the next phase of the spiral the animal swings still farther in the direction $b \rightarrow a$, and is now nearly oriented. This process continues, the animal swinging far in the direction $b \rightarrow a$ and only slightly in the direction $a \rightarrow b$, until the axis of its path coincides with the direction of the current; then the plus and minus changes cease, and there is no cause for further reaction. The general principle on which the orientation depends is this: whenever moving in a certain direction causes increased swerving, this increased swerving must show itself chiefly in the succeeding phase of the spiral, thus causing the animal to swerve farther than usual in the opposite direction.

In cases where it is the plus change which induces the reaction, the organism must, in the way just described, finally come into orientation with anterior end directed down stream. If both plus and minus changes induce reaction, then the animals become oriented in either direction, the essential point being only that the axis of the spiral coincides with the current

direction. This condition is apparently found in a number of specimens in any given culture.

2. *Reaction to Gravity; Geotaxis*.—The general features of the reaction of *Paramecium* to gravity have been described by JENSEN (1893). JENSEN further proposed a theory to account for the reactions; but at the time his work was done, the "action system"—the general complex of structural relations, movements and reactions, by which most of the behavior is brought about—was not known. JENSEN's theory could therefore take no account of this system, and I believe that in view of the known facts and of those which I shall bring forth in the present account, it can be no longer maintained. My present purpose is to describe the method by which the reaction to gravity occurs, and to show the relation of this to other reactions and to the "action system" of *Paramecium*.

The gross facts are as follows: When *Paramecia* are placed in a vertical tube, fairly free from other sources of stimuli, they swim upward, to the upper end of the tube. Control experiments show that gravity is the real directive influence. But usually some individuals in any culture show the opposite effect, swimming downward, while others do not become oriented at all. In certain cultures the majority of the individuals swim downward, or are indifferent. The reaction to gravity is easily overcome or modified by the action of other agents (SOSNOWSKI, 1899, MOORE, 1903).

JENSEN's theory to account for the reaction to gravity was as follows: The cause of the reaction is the difference in pressure upon the two sides or ends of the animal; the lower end or side is in a region of greater pressure than the upper. The greater pressure acts as a stimulus to cause the cilia on the lower side of the body to beat more strongly. As a result, the anterior end must be turned in the opposite direction (that is, upward), until it points in the direction of least pressure. The two sides are now similarly affected by the pressure, so that there is no cause for further turning. JENSEN's theory is thus an application of the typical tropism schema to the reaction to

gravity, the difference in pressure on two sides or ends of the animal being the determining factor.

Does the unoriented animal react as JENSEN supposed, by turning *directly* toward the side of least pressure? This question is not to be answered from *a priori* considerations; only actual observations of the movements of the animal in becoming oriented can give us a reliable answer. With the BRAUS-DRÜNER stereoscopic binocular such observations can be made without great difficulty. The best plan of experimentation that I have found for giving many opportunities to observe the animals at the time orientation takes place is as follows. The animals are placed in a long U-tube (Fig. 12). The two open

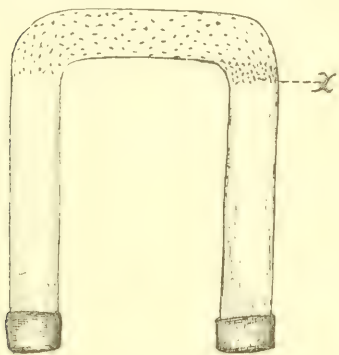


Fig. 12. Tube for study of the reaction to gravity. *x*, place where the change of direction of movement occurs.

ends are covered with rubber caps, and the tube is at first placed with free ends upward. The Paramecia collect at the free ends. Now the tube is inverted; the clouds of Paramecia at the two ends move upward, toward the cross piece of the U which is now above (Fig. 12). Arriving here, most of them do not cease swimming, but move across the cross piece of the U and even start obliquely downward. Here the reaction occurs;

they turn around and swim upward again. At this point (*x*, Fig. 12) one has at any instant a large number of specimens in the process of becoming oriented with anterior ends upward. The binocular is now brought to bear upon this region, and the method of reaction is evident. The spiral course becomes wide, the animals swerve strongly toward the aboral side, so that the anterior end is moving about in a circle; the Paramecia appear to oscillate irregularly back and forth. In other words, they are reacting in the usual "trial and error" way—"trying" successively many different positions. This is continued till they have gradually worked around into a posi-

tion with anterior end upward. The strong swerving then ceases; the animals swim upward in the usual spiral path.

Thus, observation shows that the reaction is not brought about in accordance with the tropism schema, as was supposed by JENSEN. The animal does not turn *directly* into orientation, as that theory requires, but the turning is throughout toward the aboral side, and the orientation is attained by the "method of trial and error."

What is the cause of the reaction? JENSEN's theory that it is the difference in pressure on the two sides of the animal loses whatever plausibility it may have had, when the nature of the reaction itself is known. As we have seen, the turning in the reaction is not due to differential action on upper and lower sides, but to swerving toward a side that is structurally defined—the aboral side—whatever the position of the latter with reference to gravity. Thus the difference in pressure certainly does not act in the direct way supposed by JENSEN.

Furthermore, as we have seen above (p. 467), in no other reactions of *Paramecium* is the difference in intensity of a graduated stimulus on the two sides or ends of the animal known to be the determining factor in the reaction.

On many other grounds it is highly improbable that this difference in pressure is the effective agent. The difference in pressure between the two sides is so excessively minute in proportion to the total pressure acting on the animal, that it is almost inconceivable that this difference should be perceived. The infusorians are of course under atmospheric pressure; this is equal to the pressure of a little more than 10,000 millimeters of water. As JENSEN shows, the difference in pressure between the two sides of certain of the infusoria which show the reaction to gravity is only that of 0.01 mm. of water. Hence the difference in pressure between the two sides of the organism is only $\frac{1}{1,000,000}$ of the pressure acting everywhere on the surface. Furthermore, JENSEN showed that the reaction still occurs when the atmospheric pressure is more than doubled; the effective difference in pressure would then be less than $\frac{1}{2,000,000}$ the general

pressure. When we consider the large threshold differential required for the perception of differences in pressure in known cases—for example, about $\frac{1}{10}$ in man—we can hardly believe that a differential of $\frac{1}{2,000,000}$ is perceptible by infusoria. JENSEN did not calculate this threshold differential, but said in general that the great sensitiveness here shown agreed well with the great sensitiveness to chemical, thermal and other stimuli. But the great sensitiveness assumed to exist for chemicals and heat was based on the theory that the reaction was due to the difference in intensity of the agent in question on the two sides or ends of the animals. This I have shown in previous papers not to be the cause of the reactions in question; they are due to changes in intensity brought about by the movements of the Paramecia from one region to another. The degree of sensitiveness required is therefore much less than would be necessary on JENSEN's theory, and does not approach remotely such a minuteness of threshold differential as JENSEN's view requires for the reaction to pressure.

Further, JENSEN assumes that the reaction is brought about when there is a difference of a similar order of magnitude to that above mentioned, between the anterior and posterior ends of Paramecium. Now, we know that the anterior end is much more sensitive than the posterior; this has been shown precisely for mechanical pressure. A Paramecium touched with a glass hair at the anterior end reacts violently, while the same touch or a stronger one on the posterior half of the body produces no reaction. Thus it may be considered practically certain that an increase of pressure on the posterior end such as JENSEN's theory assumes to be the effective agent would cause no reaction whatever; any reaction to the existing pressure which might occur would be due to that at the anterior end.

JENSEN makes one attempt to differentiate experimentally between the direction of gravity and the direction of decrease of pressure, and to show that the Paramecia follow the latter instead of the former. He placed Paramecia in a tube inclined to the perpendicular, and observed that, while often the Para-

mecia first swim vertically upward against the inclined wall, then turn away, and again swim vertically up till they strike it, etc., in other cases they swim obliquely upward along the wall. From this latter fact he concluded that they swim in the direction of decrease of pressure, instead of in the direction of action of gravity. It is difficult to imagine from what data or by what process of reasoning this conclusion was reached. The decrease in pressure of course takes place in an inclined tube in the same direction as in a perpendicular one, and coincides in both cases with the direction of gravity. JENSEN'S experiment was not of the least value in differentiating the two directions; indeed, so long as the pressure is due to gravity the two directions in question must coincide. If, therefore, the observations mentioned speak in the least against the view that the organisms tends to move in the lines of the direction of gravity (which, as DAVENPORT, 1897, p. 123, has shown, they do not), then they speak equally against the view that the movement is in the direction of decrease of pressure.

What then is the effective stimulus in the reaction to gravity? In the other reactions of *Paramecium* we have found that the effective stimulus is due to some change in the conditions, or, what amounts to the same thing, in the relation of the organism to the conditions. In the reactions to gravity exactly the conditions are present for the production of such changes, and the reaction is of precisely the character that might be expected from such changes as occur. The conditions are quite parallel to those found in the reactions to water currents. The changes in question are brought about through the fact that *Paramecium* swims in a spiral, swinging successively in many directions. In an unoriented specimen the upward phase of the swerving is resisted by gravity, making the motion more difficult; the downward phase is assisted, making the motion easier. The effect of these repeated changes in resistance or the ease of swimming is similar to the effect of repeated streams of water directed on a quiet animal. The result of such environmental changes is, as we know, to produce the "avoiding reaction," and this is what we see in the reaction to gravity.

The animal swerves farther toward the aboral side, and this, with the revolution on the long axis, causes it to occupy successively many different positions. When as a result of these repeated "trials" it comes into such a position that the changes causing the reaction no longer occur, the reaction ceases. Such a position is found only when the axis of the spiral course coincides with the direction of gravity. In this position the body of the animal, maintaining a constant angle with the axis of the spiral, maintains also a constant angle with the direction of gravity; changes in the relation of its swerving to the direction of gravity, therefore, no longer occur. To constant conditions *Paramecium* quickly becomes acclimated, so now reaction no longer takes place.

Whether the anterior end is directed upward or downward depends upon whether the plus or minus change in resistance induces the reaction. If the minus change—the change from the greater resistance of the upward swing to the less resistance of the downward swing—is the effective stimulus, then the animal will become oriented with the anterior end upward, for every time it swerves downward the reaction is induced, causing it to "try" many new positions, while when it swerves upward no reaction is induced, and it retains the position reached. This is apparently the usual condition of affairs. On the other hand, if it is the plus change—the change from less resistance to greater resistance—that causes the reaction, the animal will become oriented with anterior end downward. To both cases we could apply the detailed analysis given in the account of the reactions to water currents, above.

Thus as to the nature of the effective stimulus in gravitation, our analysis leads to results agreeing with the conclusions of DAVENPORT (1897). This author holds that the reaction to gravity is due to the fact that the organism "experiences greater resistance (friction + weight) in going upward even to the slightest extent than in going downward (friction - weight)" (*l. c.*, p. 122). What I have set forth above is the way in which this difference in resistance acts in orienting the organism.

The stimulus induced by the variations in the resistance due to gravity is of course a very light one, and observation shows that it is easily modified or masked by other stimuli. Chemical, mechanical and electrical stimuli overcome the reaction to gravity, hence the necessity of having the *Paramecia* in nearly pure water and in a clean tube if the reactions to gravity are to be seen clearly. If these conditions are not fulfilled, the *Paramecia* may collect in any part of the tube, through reactions to chemical stimuli, and to contact with solids. It may perhaps be said in general that the reaction to gravity shows itself only when the animal is not subjected to other effective stimuli.

JENSEN (*l. c.*) showed that when placed on the centrifuge *Paramecium* reacts with regard to the direction of the centrifugal force in the same way as to gravity. The animals orient themselves and swim in the direction opposite to that in which the centrifugal force tends to carry them. In these experiments the conditions are of course present for the same sort of reactions that we find under the action of water currents and of gravity. In one phase of the spiral course the movement of the unoriented animal is assisted by the centrifugal force, in another resisted; the changes thus produced lead to reaction and orientation in the way already described.

Summary.—The reactions to water currents ("rheotaxis"), to gravity ("geotaxis") and to centrifugal force are in *Paramecium* essentially the same, and due to similar conditions; they may be summed up as follows: The unoriented individual is subjected, owing to its spiral course, to repeated changes of pressure and of the resistance to its movements; in one phase of the spiral the motion is assisted, in another resisted. These changes induce the usual reaction; through the consequent increased swerving toward the aboral side, with the revolution on the long axis, the animal occupies successively many different positions, till one is found in which these changes no longer occur, when there is no further cause for reaction. Such a position, in which the relation of the movement to the resistance remains constant, is found only in orientation with the axis of

the spiral path coincident with the direction of the force in question. Under the action of the three agents named, as a rule it is the minus change that induces reaction; hence the animal directs itself against the operation of the forces at work.

B. Behavior during Conjugation.

The behavior during conjugation is not brought about through the avoiding reaction, yet the conditions determining it seem of the same character as those determining behavior produced through the reaction named, so that it should be considered in relation with the latter. It is not my purpose to give here a full account of the behavior during conjugation, but merely to point out the part played in this behavior by the usual "action system" of *Paramecium*, above set forth.

Paramecia during a period of conjugation are perhaps in a "physiological state" differing from the usual state, so that they react differently from usual, uniting in pairs. Yet it is remarkable how much of their behavior at such times is due to precisely the same features that are always present, taken in connection with a physical modification of the body substance. I have not thus far been able to observe at such times any method of reaction differing from the usual ones. The factors bringing together two individuals seem to be chiefly the following.

1. At these periods of conjugation the oral surface of *Paramecium* is adhesive, through some physical modification of the protoplasm. As a result of this modification other *Paramecia* coming in contact with the oral surface become attached. The position of the two *Paramecia* is of no consequence, nor the way in which the contact is brought about, provided only that one animal comes in contact with some part of the oral surface of another. As a result of this fact, the individuals in a crowded culture become stuck together in all sorts of bizarre ways, and evidently without any previous definite reaction on the part of the individuals concerned. Two specimens will be seen feeding on the bacterial zoogloea and moving in opposite directions over its surface; one crosses by chance the path of the other,

and in passing its posterior end drags across the oral surface of the latter. Thereupon they stick together, and a struggle ensues, each individual trying to pursue its forward course and not succeeding, till one finally drags the other one backward (Fig. 13, at the upper left hand corner). The second speci-



Fig. 13. Irregular adhesion of individuals, observed in cultures of *Paramecia* in which conjugation was taking place. These groups move about irregularly, remaining attached, in spite of the struggles of the individuals.

men may be dragged about through the water or over obstacles of all sorts, till finally the adhesion gives way and they separate. Specimens thus become adherent in every possible way, provided merely that some part of the oral surface of one of the individuals enters into the adhesion. Many such cases are clearly not early stages of any ordered conjugation, and they often separate after one individual has been dragged about for some time much against his struggles.

Again, often more than two individuals thus adhere; groups of three, four or five are seen, adhering in all sorts of irregular ways, and apparently struggling to free themselves. A number of such cases of irregular adhesion are shown in Fig. 13, from a culture in which conjugation was taking place freely. It is evident that such groups as are shown in this figure cannot be interpreted as due to any will or desire of the

animals, and this becomes still more evident when one observes the accidental manner in which they are formed, the way in which the individuals are dragged about against their efforts, and their struggles to free themselves—at times resulting successfully. I have even seen moribund individuals, and individuals undergoing fission thus attached irregularly to the oral surface of other specimens.

2. A second important factor in bringing about conjugation is found in the usual ciliary movements of the animals and in the currents produced by these movements. As we have seen in the foregoing pages, there is a strong current passing backward along the oral side of *Paramecium*, so that there is a tendency for all sorts of objects suspended in the water to be carried to the oral groove. This tendency is of course operative on other *Paramecia* in the neighborhood as well as upon lifeless objects. In the case of two *Paramecia* close together this tendency is of course reciprocal; each tends to draw the other to its own oral groove. Thus if two *Paramecia* are swimming along close together, there is a strong tendency, through their usual movements, for them to come together with oral surfaces in contact. Under ordinary conditions this is often seen, but does not lead to conjugation, because the oral surfaces are not adhesive. But when the oral surfaces are adhesive, as we know them to be at periods of conjugation, then the animals stick together. The remainder of the process falls outside the field of "behavior." The relations just pointed out show why in a conjugating culture so many more individuals are found in contact by their oral surfaces than in the irregular ways shown in Fig. 13; the irregular adhesions occur only through unusual accidents.

Thus when the oral surfaces of *Paramecia* become adhesive, the usual movements lead to attachment by these surfaces, such as we find in conjugation. All the phenomena seem to be intelligible on the basis of these factors alone, though it may be possible that there are certain modifications of the usual behavior in periods of conjugation.

C. Responses to Stimuli not brought about through the "Avoiding Reaction."

The behavior which we have thus far considered is brought about chiefly through the avoiding reaction; the general method is that of "trial and error." Though the most important features of the behavior of *Paramecium* are produced in this way, there are certain other reactions in which the method of "trial and error" does not play the chief, or at least the only part; in these the relation of the direction of movement to the source of stimulus is, in certain features at least, more direct. These reactions we shall take up next, though only with the reaction to the electric current shall we deal here in detail. A list of these reactions was given on page 450. Local contraction of the body as a response to stimulation has been dealt with sufficiently above (page 457), and in the paper of STATKEWITSCH (1903). MASSART (1901) gives a thorough study of the discharge of trichocysts as a response to various stimuli, while STATKEWITSCH (1903) gives details as to the production of this reaction by induction shocks. The reaction to contact by coming to rest has been described in detail in a previous paper by the present author (JENNINGS, 1897), and in a more recent paper by PÜTTER (1900). These matters, then, we need not consider further here.

1. Forward Movement as a Response to Stimulation.

In a previous paper (JENNINGS, 1900) I showed that many Infusoria respond to a stimulus which affects only some other part of the body than the anterior end, by moving forward. I did not succeed in showing this for *Paramecium*, owing to difficulties of technique in working with so small an animal. In the meantime ROESLE (1902) has observed that when a specimen is stimulated at about the middle of the body by collision with another specimen, it responds by moving forward. I have recently been able to confirm this result experimentally. A small glass rod may be drawn out so fine that the tip is hardly visible under a magnification such that the differentiations in the body of *Paramecium* are conspicuous and cilia are plainly

seen. With the tip of such a rod it is possible to stimulate *Paramecium* locally, without jarring the animal as a whole. It is then found that a mechanical stimulus back of about the anterior one-third causes a movement forward. It is notable that at the anterior end the lightest touch produces a strong avoiding reaction, whereas an equally light stimulus elsewhere produces no reaction whatever. I was not able to confirm with the rod ROESLE's view that the region about the mouth is especially sensitive, but this seems highly probable on general principles, as well as in view of ROESLE's results; the technical difficulties of reaching precisely the region about the mouth with the rod are very considerable.

A very powerful stimulus even on the posterior part of the body induces the avoiding reaction. But this may be due to the mechanical transmission of the shock to the anterior end.

Apparently a very light, unlocalized stimulus likewise produces forward swimming, as I noted in a previous paper (1899, *a*, p. 104). This is true of a slight jarring of the vessel containing resting individuals. ROESLE (1902) states that an induction shock sometimes has the same effect, though as STATKEWITSCH (1903) shows, this stimulus usually produces the avoiding reaction.

2. Reaction to Electricity.

Part Played by the Action System.—The reaction to the electric current presents certain features not found in the reactions to other stimuli. According to the account of this reaction in the foundational paper of LUDLOFF (1895), the cilia on the cathode half of the body of *Paramecium* strike forward, those on the anode half backward. The inevitable result is that any specimen not in line with the current will be turned directly around, until the anterior end is toward the cathode. The reaction seems, according to this account, to be much simpler and more schematic in character than the reactions to other stimuli, the characteristic "action system" seeming to play no differential part. But the recent papers of PEARL (1900), PÜTTER (1900) and WALLENGREN (1902, 1903) show that the reac-

tion to the electric current is in many ciliates more complex and less schematic than had been supposed. As first brought out in the paper of PEARL (1900), there seems to be an attempt by the animal to react in the same way to the electric current as to other stimuli (PEARL's "reflex factor"), but this is modified or masked by certain effects peculiar to the current (PEARL's "forced movements"). Cilia of different parts of the body under the influence of the current thus differ in their method of action and force of stroke. WALLENGREN (*l. c.*) shows that whether anodic, kathodic or transverse electrotaxis is produced depends upon the peculiar action of the cilia of certain regions of the body. Thus the "action system" of the organisms does play a part in determining the reaction to the electric current, though not so exclusive a part as in the reactions to the stimuli met under natural conditions of life. The corresponding relations have never been brought out for *Paramecium*;¹ this I shall try to do in the following.

PEARL (1900) confirmed LUDLOFF's schematic account of *Paramecium*, though at the same time he showed, as noted above, that in certain other ciliates the "action system" (his "reflex factor") does play an important part in determining the reaction to the electric current. Though the results of LUDLOFF and PEARL on *Paramecium* are correct so far as they go, they are incomplete. The "action system" does in reality play a much larger part in determining the reactions to the electric current than would appear from the accounts of the two authors named. This is most clearly seen in the fact that when the anterior end is directed toward the anode at the moment the current is made (Fig. 14, *b*) the animal always reaches the position of orientation with the anterior end to the cathode by turning toward the aboral side, as in the reactions to other stimuli. Under these conditions the cilia of both the oral and aboral sides beat backward in the anterior half of the body (Fig. 14, *b*); since the cilia of the oral groove are more powerful than the opposing

¹ It is somewhat peculiar that these relations are not dealt with in the recent extensive and valuable paper of STATKEWITSCH (1903, *a*).

aboral ones, they turn the organism toward the aboral side. But this is aided by the fact that the cilia of the aboral side of the anterior half of the body strike obliquely toward the oral side. So far then as the anterior half of the body is concerned, this reaction is the same as that produced by other stimuli. In the posterior half, directed toward the cathode, another factor plays a part, to be taken up later; but this has under the present conditions no effect on the reaction.

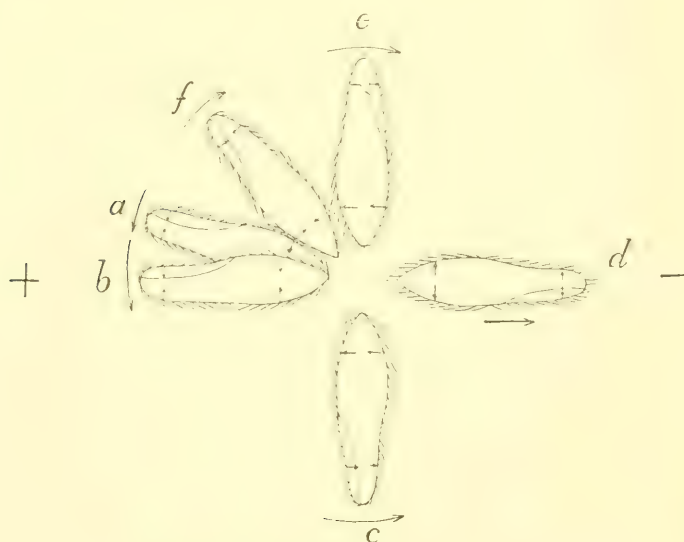


Fig. 14. Diagram representing the action of the cilia and the direction of turning in *Paramecia* occupying different positions with relation to the electric current. The small arrows within the outlines of the body represent the direction in which the cilia of the different regions tend to turn the animal; the larger external arrows represent the actual direction of turning. In all positions from *a* to *d* the turning is toward the aboral side; at *e* it is toward the oral side.

Even when the animal lies in a very slightly oblique position, so that orientation would be reached somewhat more quickly by turning toward the oral side (Fig. 14, *a*), the turning is still toward the aboral side, the strong oral cilia striking backward and driving the animal toward the aboral side. Further, when the animal is transverse to the current and the aboral side is toward the cathode (Fig. 14, *c*), the turning is of course toward the aboral side, as inspection of the figure shows it must

be. Indeed, in any position from *a* through *b* and *c* to *d*, Fig. 14, the animal attains orientation by turning toward the aboral side, as in reactions to other stimuli. These results follow even when the movements of the cilia are precisely those described as typical by LUDLOFF, the greater effectiveness of the oral cilia determining the direction of turning.

On the other hand, if the animal is transverse to the current with the oral side toward the cathode (Fig. 14, *e*), it turns directly toward the *oral* side, until the position of orientation is reached. In this turning toward the oral side the electrotactic reaction differs from the motor reactions to other stimuli, the factor peculiar to the action of the electric current playing here the essential part. In the typical case where the cilia act as described by LUDLOFF, all the cilia tend to produce the turning toward the oral side, as Fig. 14, *e*, shows.

Between the position shown in Fig. 14, *e*, in which the animal turns toward the oral side, and that in Fig. 14, *a*, in which it turns toward the aboral side, there is of course an intermediate position in which the tendencies to turn in the opposite directions are in equilibrium. In such cases the animal retains its position until the normal revolution on the long axis has occurred, bringing the body into the position shown in Fig. 14, *f*, with aboral side to the cathode. The animal then of course turns at once toward the aboral side, into the position of orientation. A similar method of reaction in certain positions has been described by PEARL (1900, p. 101, "type III") for *Colpidium*, and by WALLENGREN (1902, p. 365) for *Opalina*. The tendency to turn in two opposite directions at once, as it were, so that the animal no longer reacts in a co-ordinated way, is very characteristic for the reaction to the electric current, distinguishing this reaction from all others.

Altogether, in nearly three-fourths of all possible positions the animal attains orientation by turning toward the aboral side; that is, the "action system" of *Paramecium*—PEARL's "reflex factor"—determines to this extent the reactions to electricity, as it does still more completely the reactions to other stimuli. In practical experimentation with free swimming Para-

mea the turning toward the aboral side plays even a larger part than is indicated in the discussion just given. Thus, if the current is frequently reversed, the *Paramecia* practically always become re-oriented by turning toward the aboral side, since after the reversal the anterior end is directed to the anode as in Fig. 14, *b*; in this position, as we have seen, the turning is always toward the aboral side. It is only by taking special pains to close the current when the animal is in such a position as is shown in Fig. 14, *c* that it can be caused to turn toward the oral side. The result is then due to an effect peculiar to the current, which will be taken up later.

The "action system" in *Paramecium* further plays a part in the reactions to electricity in the fact that the response on breaking the circuit, and the response to a single induction shock, take the character of the typical "avoiding reaction." This response at the breaking of the circuit is described by PEARL (1900, p. 113); the response to induction shocks by STATKEWITSCH (1903, p. 48).

Again, the "action system" of *Paramecium* plays a part in the fact that the path followed during the reaction to the constant current is a spiral of the usual sort, the animal revolving to the left and swerving toward the aboral side. Thus there is during the reaction to the current an obliqueness in the stroke of the cilia similar to that found under usual conditions. Certain variations in the spiral path under the action of the electric current will be taken up later.

Peculiarity of Reaction to the Electric Current.—On the other hand, it is clear that a factor exists in the reaction to the electric current which is not found, so far as known, in the reactions to other stimuli—a factor not supplied in the "action system" as observed in the movements under the natural conditions of existence. This is the factor shown in the turning toward the oral side under certain conditions; the factor that causes the animal to try at times to turn in two opposite directions at once—PEARL'S "forced movement factor." What is its nature?

The characteristic phenomenon of the reaction to the elec-

tric current is the contrasted action of the cilia in the cathode and anode regions of the body (Fig. 14), as described by LUDLOFF (1895). But it is to be observed that the action of the cilia in the anode region is identical with that which occurs under the influence of any other stimulus. The work of ROESLE (1902) and STATKEWITSCH (1903) shows that under induction shocks the stimulation is primarily at the anode, and that the effect of this stimulation is similar to that of stimulation by other means; the cilia are reversed for a short time, so that the animal swims backward; then it starts forward in a new direction (STATKEWITSCH, 1903). Under the constant current, after the circuit has been closed and the conditions have become constant, the anode cilia are directed backward, as under usual conditions, so that so far as they are concerned the animal swims forward in the normal way. It is then in the continued reversal of the cathode cilia that the peculiar action of the current manifests itself; these cilia oppose the normally acting anode cilia, giving rise to the conflict in direction of turning and of progression that is so striking a factor in the reactions to electricity. LUDLOFF's account of this peculiar action of the cathode cilia is excellent, but certain points brought out by LUDLOFF are not included in the schema usually copied from his work, and this has given rise to certain misconceptions. This has been shown in the recent valuable paper of STATKEWITSCH (1903 *a*). My own results confirm those of STATKEWITSCH on this point; since they were obtained quite independently of the work of STATKEWITSCH,¹ and by a different method of experimentation, I will set them forth. The essential point is that the reversal of the cilia in the cathode region of the body does not typically include just half the body, as is usually set forth. On the contrary, it begins in a weak current with a very slight effect limited to the point of the cathode end of the body, and as the current becomes stronger it spreads gradually backward, until it finally includes almost the entire body. STATKEWITSCH

¹ My experimental work was completely finished and the first draft of this paper written when STATKEWITSCH's paper appeared.

(1903 *a*, p. 92) determined this by direct observation of the cilia on animals in viscous media of various sorts, inventing a number of new media for this purpose. My own results were obtained by observation of the currents produced by the cilia. These observations were made by the use of India ink in the water containing the animals, as set forth above (p. 442); they add certain features to the results set forth by STATKEWITSCH.

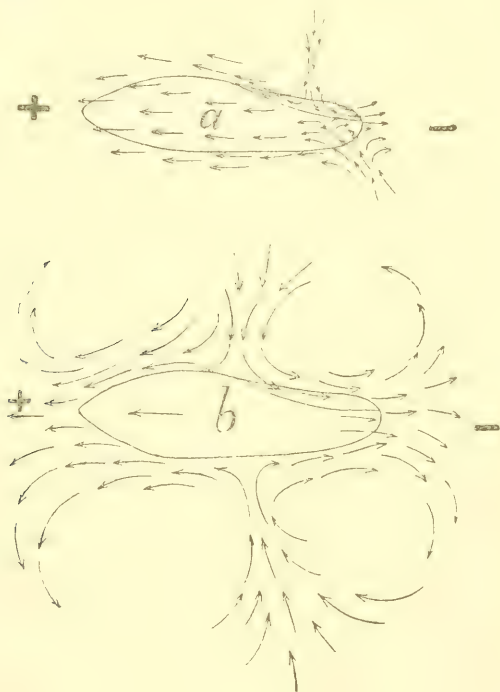
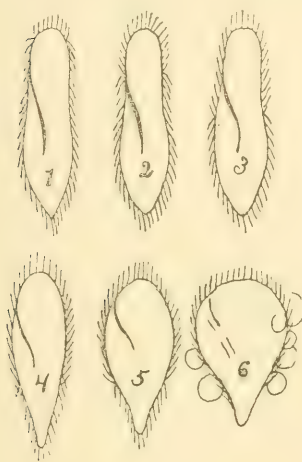


Fig. 15. Currents of water produced by the action of the cilia in the reaction of *Paramecium* to the electric current. *a*, electric current weak, water currents reversed only at the anterior tip—most markedly in the oral groove; *b*, electric current strong. The arrows show the direction of the water currents.

With a weak electric current the ciliary currents, after orientation is reached, are everywhere backward. At the very anterior tip (directed to the cathode) the currents are perhaps a little less strongly backward than when the animal is not subjected to electricity. This agrees with the results of LUDLOFF and of STATKEWITSCH (1903 *a*), who found that in a weak cur-

rent only the cilia at the cathode tip are reversed (Fig. 16, 1). An additional feature, to be observed from the movements of the ciliary currents, is that in the oral groove the cathode effect is more marked than elsewhere, and shows itself by repeated reversals of the ciliary current in the anterior part of this region, lasting but an instant.

With a stronger current the effective stroke of a part of the cilia of the anterior region of the body is reversed, so as to be forward. At first this includes only a small part of the anterior region of the body, and this result is reached first in the



oral groove, where a water current passes continually forward even when the electric current is so weak that over the remainder of the anterior part of the body the water currents are still backward or at rest (Fig. 15, *a*). As the electric current is made stronger, the currents pass forward over the entire anterior half of the body. This is the stage usually considered typical, though as STATKEWITSCH (1903 *a*, p. 93) points out, it is only one point in a series of continuous

Fig. 16. Different stages of the reaction of the cilia to the electric current, after STATKEWITSCH (1903 *a*). The cathode is conceived to be above, the anode below. In a weak current, only a few cilia at the tip of the cathode end are reversed (1). As the current becomes stronger (2, 3, 4, 5, 6) more and more of the cilia are reversed, until in the strongest currents practically all of the cilia strike forward.

changes. At this stage there is still an alternation at intervals in the direction of the effective beat of the cilia of the anterior half of the body, giving the movement a jerky character. As the electric current is made stronger the forward water currents on the anterior half of the body become constant and more powerful; the currents on posterior and anterior halves separate at about the middle of the body, and water is drawn from all sides

to supply them, making the animal the center of a sort of cyclonic disturbance in the water (Fig. 15, *b*), which gives a most extraordinary appearance. At this stage the forward movement of the animal is much retarded, owing to the strong backward stroke of the cilia on the anterior half of the body.

With a still stronger electric current the forward ciliary currents in the anterior (cathodic) region of the body become still more powerful and extensive, seeming to begin even behind the middle, though the precise boundaries of the two sets of currents are very difficult to determine by this method of observation. There comes a period when the effect of the two sets of currents are equal, and the animal neither advances nor retreats, but retains its position, revolving rapidly on the long axis. It is clear that the forward stroke of the anterior cilia just balances the backward stroke of the posterior cilia. Often the two sets of cilia alternate in obtaining the upper hand; the animal is driven backward a distance, then forward again. If the electric current is made still more powerful, the forward currents in front become still stronger and more extensive; they gain the upper hand permanently, and the animals are driven backward toward the anode.

For stronger electric currents it is not possible to determine by observation of the ciliary currents the distribution of forward and backward striking cilia. But this has been determined from direct observation by STATKEWITSCH (1903, *a*); his results are shown in Fig. 16. The reversal of the cilia, beginning with a weak electric current at the cathodic tip, extends backward as the current becomes stronger till it finally includes practically the entire body surface.

In view of these results, the known facts as to the reaction to the electric current may be formulated as follows. First, the current stimulates in the same manner as any other stimulus; this stimulation has origin at the anode. Second, the results of this stimulation are interfered with or overcome by an effect peculiar to the electric current, and having origin at the cathode. This peculiar effect is shown in a progressive reversal of the cilia, beginning with a weak current at the cathode tip, and

gradually extending toward the anode end, until with a strong current it affects almost or quite the entire body. Without this second factor, the reaction to the electric current would apparently take place in the same way as the reaction to gravity or to currents of water. The first factor mentioned corresponds to PEARL'S "reflex factor," the second to his "forced movement factor."

Thus in the reaction to the electric current the point especially demanding explanation is the cathodic reversal of the cilia; it is this which distinguishes this reaction from all others. As STATKEWITSCH (1903, *a*, p. 79) has emphasized, "the reaction of the cilia is the first and fundamental phenomenon of galvanotropism." Any theory of the reaction to the electric current is of value just in so far as it promises to aid us in understanding the peculiar action of the current on the cilia. Theories which attempt to account for electrotaxis on certain general considerations, without taking into account the effect on the cilia, are at the present time anachronisms; they close their eyes to the real problem that needs solution.

As to the fundamental nature of the change in the protoplasm that induces the cathodic reversal of the cilia, which forms the distinctive feature of the reaction to the electric current, the conclusions drawn from the thorough and extensive work of STATKEWITSCH (1903, *a*) are most worthy of consideration. For details reference must be made to the original work of STATKEWITSCH;¹ we may say here that the author comes to the conclusion, after extensive experimentation as to the chemical and physical effects of the electric current on the organisms, that the current disturbs the usual equilibrium of the processes of metabolism in such a way as to produce a change in the normal backward stroke of the cilia, in the manner described above (*l. c.*, p. 158)—this change beginning at the cathode end, and progressing, as the current is made stronger, over the entire body.

¹ A German translation of parts of STATKEWITSCH'S Russian text is to appear, I understand, in VERWORN'S *Zeitschrift für Allgemeine Physiologie*.

Cause of Backward Swimming in Strong Currents.—The observations described above on the direction of the effective beat of the cilia as the current becomes stronger throw light on the disputed question as to the cause of the swimming backward toward the anode in a strong current. LUDLOFF (1895) explained this backward movement as due to the fact that in a strong current the effectiveness of the reversed stroke of the anterior (cathodic) cilia becomes increased, till it overcomes the forward effect of the posterior cilia. According to LUDLOFF's view, then, the animal swims actively backward in a strong current, just as it swims actively forward in a weak current. On the other hand PEARL (1900, p. 123) holds that in a strong current the animals are borne passively backward to the anode by the cataphoric effect of the current—the electrical convection—while their active movements tend to carry them to the cathode. In other words, he holds that in a strong current the electrical convection becomes more effective than the stroke of the cilia, thus carrying the animal backward. DALE (1901, p. 354) holds the same view. WALLENGREN (1902) adopts this explanation, for *Opalina*, without expressing an opinion in regard to *Paramecium*. Which of the two explanations is correct?

As the account given on preceding pages (pp. 490-492) shows, the observations on the direction of the effective beat of the cilia are throughout in accordance with the explanation given by LUDLOFF, and no other factor is required to account for the phenomena which actually occur. When the animal is swimming backward to the anode the effective beat of a large portion of the cilia is demonstrably forward, producing currents equal or superior to those due to the backward stroke of the other cilia. This forward stroke of the anterior cilia must inevitably tend strongly to drive the animal backward, so that at the best only a very small part in the phenomena could possibly be attributed to the electrical convection. The direct impression from observations is that the result is fully accounted for without bringing the electrical convection into the matter at all.

The further question arises as to whether the electrical

convection is competent to produce the effect ascribed to it on the view of PEARL and DALE. With the strength of current used, is the electrical convection sufficiently powerful to carry the bodies of Paramecia, considered merely as pieces of material of a certain size and weight, toward the anode at the rate at which the Paramecia move backward? Observation shows that even smaller, non-living particles are not carried toward either pole at any such rate. Further, Paramecia that have been killed in ether, chloroform, chloretone or formalin are not moved to either electrode by the electrical convection. BIRUKOFF (1899), who maintains the efficacy of electrical convection, endeavors to explain the fact last cited as follows. The dead Paramecia do not remain suspended, but sink to the bottom, and it is a necessary condition for the effective operation of electrical convection that the solid particles in question should remain in suspension.

Obviously then in order to test this matter we must arrange experiments in such a way that the dead Paramecia shall remain for some considerable time suspended. This is easily done by placing them in a vertical tube, or by placing the slide bearing the Paramecia in a vertical position. The electrodes are then introduced at the upper and lower ends of the tube or preparation. The Paramecia sink slowly through the water, and thus remain a long time suspended, not being in contact with any solid objects till they reach the bottom.

With living specimens under these conditions the reactions are identical with those in horizontal preparations. If a weak current is used, the Paramecia hasten to the cathode, both when this is at the upper, and when it is at the lower end of the tube. If a stronger current is used, and the upper end of the preparation is made the anode, the infusoria swim backward against the pull of the gravity to the anode, at the upper end. With lifeless Paramecia on the other hand no such effects are produced. The dead animals simply sink steadily, whatever the strength of the current, in spite of electrical convection toward cathode or anode.

Thus whatever it is that causes the Paramecia to move

backward to the anode in a strong current is competent to lift the animals against the force of gravity. The electrical convection is not competent to produce this result. It is therefore evident that the electrical convection is not the essential agent in producing the movement of *Paramecium* backward to the anode. The observations previously detailed show clearly what *is* the agent producing this result.

BIRUKOFF (1899) held even that the usual movement to the cathode was produced by the cataphoric effect, or electrical convection. This had of course been disproved long before the paper of BIRUKOFF was written. As an additional disproof, we may note that the experiments just described show that the electrical convection is not competent to produce the effect observed in the movement to either cathode or anode. It is to the movements *of the cilia* brought about by the electric current that we must turn for the real factors producing the movements to cathode or anode.

Relations between Contact Reaction and Reaction to Electric Current.—In a previous paper (1897) I described what I called an interference between the contact reaction ("thigmotaxis") and the reaction to the electric current, and in a later paper PÜTTER (1900) considerably extended our knowledge of the phenomena in question. The interference described consisted, so far as *Paramecium* is concerned, essentially in the fact that specimens showing the contact reaction respond less readily to the electric current than do free specimens, and the response, when it occurs, is intermittent. For *Stylonychia*, PÜTTER held that a further effect was evident, in the fact that thigmotactic specimens take up a transverse position with respect to the electric current, while the free specimens swim directly to the cathode.

I wish to bring out here certain further points in regard to the interference between the contact reaction and the reaction to the electric current. These are the following:

1. In my previous paper I described this interference only for the case of *Paramecia* in contact with a mass of detritus. But the *Paramecium* need not be in contact with such a mass in

order to show the interference described. It occurs also when the animals are in contact with a clean glass surface, or the surface film of water. This is particularly evident when the *Paramecia* are subjected to a moderately strong current on the slide in a thin layer of water, without a cover. They swim as usual toward the cathode. But when a specimen in its spiral course comes against the glass slide or the surface film, it at once stops. It may stop only an instant, or it may remain at rest for some time; or it may show certain peculiar movements, to be described later.

2. The effect of thigmotaxis appears not merely in a decrease in sensitiveness to the current, but in a change in the method of reaction to the current. PÜTTER (1900) showed that in various *Hypotricha* individuals in contact with a surface take, in the current, a nearly transverse position with the left side (bearing the peristome) to the cathode, while free swimming individuals become oriented with anterior end to the cathode.

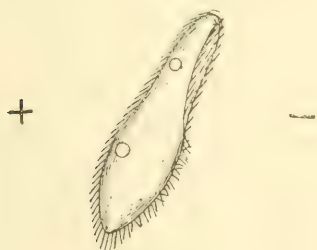


Fig. 17. Transverse or oblique orientation of *Paramecium* to the electric current when in contact with a surface.

Similar relations are to be observed in *Paramecium*, though less frequently than in the *Hypotricha*, because *Paramecium* is less often in contact with the surface. But when a large number of individuals are subjected to the current in a thin layer of water (with or without a cover glass), the phenomena are evident. The free specimens swim as usual, with anterior ends to the

cathode. Those that come in contact with the surface film or the glass, stop, as described above. If they do not quickly resume the forward course, they soon take up a position nearly transverse to the current, with the oral side or peristome directed toward the cathode (Fig. 17). In this position they may either remain quiet, or may move forward transversely (or obliquely) to the current, keeping in contact with the surface. The effective beat of the cilia, as determined by the movements

of the particles of India ink, is now everywhere backward, save in the oral groove, where it is usually forward, though at intervals it here passes backward for a moment.

If while in this position the direction of the current is reversed, so that the oral surface is toward the anode, the oral cilia strike strongly backward. This has one of two effects. Sometimes it causes the animal to be detached from the surface; in this case it turns toward the aboral side until the anterior end is directed to the cathode, then it swims forward in that direction, like other free swimming specimens. Or the animal may still remain in contact with the surface; in this case it turns toward the aboral side, until the peristome or oral surface is again directed toward the cathode. Then it remains quiet, or resumes its forward movement transverse to the current. In cultures where the specimens are much inclined to be thigmotactic, one often observes in this way marked transverse electrotaxis in a large number of individuals; by repeatedly reversing the current they can be driven from one side of the preparation to the other and back again, always transversely or obliquely to the current.

ROESLE (1902) observed that *Paramecium* reacts much more readily to induction shocks when the peristome is directed toward the anode than in other positions. ROESLE interprets this as showing that the peristome is more sensitive than other parts of the body surface. While this conclusion is *a priori* very probable, I am not sure that the facts cited really demonstrate it. When the constant current is made, the animal lying against a surface with peristome to the cathode, there is a reaction, which is, however, ineffective in causing a movement of the animal's body. The reaction consists in a weak reversal of stroke of the oral cilia, as is shown by the forward movement of the particles of India ink in the oral groove. This forward stroke of the oral cilia has very little locomotor effect, and does not overcome the attachment of the animal to the surface; it could not be observed without the presence of the particles of India ink. It is possible that this reaction occurs also with induction shocks, and escaped observation, owing

to the fact that ROESLE used no method of rendering the currents visible. When the circuit is closed with the peristome to the anode, on the other hand, the oral cilia strike strongly backward, and this has a powerful locomotor effect, driving the animal forward, or, if the current continues, turning it toward the aboral side. ROESLE's observations are then fully explicable on the basis of the known action of the current on the cilia, as described first by LUDLOFF, together with the stronger locomotor effect of the oral cilia when striking backward, a difference that is evident in many ways. I must then agree with the conclusion of STATKEWITSCH (1903), reached on other grounds, that the results of ROESLE do not demonstrate the greater sensitiveness of the peristome.

Thus we find under certain circumstances a "transverse electrotaxis" of *Paramecium* under the action of the constant current, as in many other infusoria. This transverse orientation is of course of an entirely different character from that obtained by STATKEWITSCH (1903 *a*, pp. 24-32), with rapidly alternating currents.

3. In a strong electric current the contact reaction causes not merely a stoppage of the forward course, but actual swimming backward. If the *Paramecia* are in a thin layer of water, through which a rather strong current is passed, all the specimens that are not in contact with upper and lower surfaces swim forward, in the somewhat cramped manner, as if against resistance, that is characteristic of the swimming in a strong current. But when a specimen comes in contact with the glass surface below or the surface film above, it begins to swim backward. This may last for but an instant, while the accidental contact continues, or if the animal remains in contact the backward swimming continues a long time. If a very thin layer of water is used, so that the *Paramecia* can hardly avoid coming in contact with a surface, most of them swim backward, though as soon as a specimen becomes free from the surface, it darts forward. With a slightly thicker layer of water, often about half the individuals are free and swim forward, while the other half are in contact and swim backward. The same individual

may alternate frequently in the direction of swimming, according as it comes in contact with the surface, or becomes free from it. To obtain these results in a sharply defined way, it is necessary to vary the strength of current until exactly the proper intensity is found.

The cause of this peculiar effect of contact seems to be as follows: PÜTTER (1900) has shown that one effect of the contact reaction is to cause the cilia of the region posterior to the place of contact to cease effective action. In the strong current the cilia of the anterior half of the body tend to drive the animal backward, while the posterior cilia force it forward; the latter are a little the more effective, so that the animal on the whole moves forward. In the spiral course the body, swerving toward the aboral side, comes in contact with the surface at about its middle. Thereupon, in accordance with the observation of PÜTTER, above mentioned, the cilia behind this spot, driving the animal forward, cease to beat, while the cilia in front of this spot, driving it backward, continue their action. Hence the anterior cilia now gain the upper hand, forcing the animal backward.

In his recent valuable papers (1903, pp. 46-47; 1903 *a*, pp. 46-56), STATKEWITSCH maintains that there is no real interference between the contact reaction and the reaction to the electric current, but that the animal in contact with a solid is reached only by a weaker current than the free swimming individuals, hence it reacts less markedly. Animals showing the contact reaction are usually in contact with a heap of detritus; STATKEWITSCH holds that the electric current divides, a portion of greater intensity passing through the water, a weaker portion through the heap of detritus and the Paramecium.

This simple physical theory would of course be very satisfactory if it explained the observed facts, but this it does not do. It is based on the assumptions (1) that the so-called interference is shown only when the animal is in contact with a heap of detritus; (2) that the interference appears only as a weakening of the reaction, not as a change in its character. Both of these assumptions, as I have shown above, are

incorrect. As to the first one, the *Paramecia*, as we have seen, show the interference described even when the animal is in contact only with a clean glass surface, or with the surface film of the water. It is evident that this cannot be explained as due to the dividing of the current and the passage of a weaker portion through the object with which the animal is in contact. STATKEWITSCH's observations on this phenomenon (1903 *a*, pp. 45-52) were made only on individuals in contact with a bit of detritus, and he assumes that this is a necessary condition for the production of the supposed interference.

As the second assumption mentioned, I have shown above that the contact reaction produces not a mere weakening of the effect of the electric current, but actual changes of a most decided character in the way the reaction occurs. *Paramecia* in contact with a glass surface or the surface film take up a transverse position, or move backward, in the same current which produces forward movement in free swimming specimens. These effects cannot possibly be explained as due to the dividing of the current into weaker and stronger portions, as supposed by STATKEWITSCH.

PÜTTER (1900) had already set forth that in *Stylonychia* the contact reaction has the effect of producing a transverse orientation in the electric current. STATKEWITSCH, however, tries to show that this transverse orientation is merely the effect of a weak current. But when one examines attentively his evidence for this (1903 *a*, pp. 43-44) it seems apparent that all the specimens which showed transverse orientation were in contact with a surface, and he does not mention the existence of transverse orientation in free swimming specimens. Thus his results are equally well explained on PÜTTER's view that the transverse orientation is due to the contact reaction. In *Paramecium* STATKEWITSCH expressly states repeatedly (for example, 1903 *a*, p. 57) that the effect of the weak current is to cause movement toward the cathode, and he never in his extensive and thorough study of the reaction of *Paramecium* to electricity observed transverse orientation to the constant current. The transverse orientation of *Paramecia* that are in contact, described

above, cannot then be accounted for as due to the weakening of the current affecting them. This is true *a fortiori* of the swimming backward of individuals that come in contact with a surface, for such swimming backward occurs under other conditions only in *stronger*, not in weaker, currents. There is no escape from the conclusion that the contact reaction interferes with and modifies in a striking manner the reaction to the electric current.

STATKEWITSCH's view that the supposed interference between the effects of the two stimuli is to be explained in the simple physical way he sets forth seems based largely on an *a priori* conviction that the electric current *must* always produce the same reaction when it acts upon the same organism with the same strength (see for example STATKEWITSCH, 1903, p. 46). This conviction appears in a most curious way in his attempts to demonstrate the correctness of his view. In his earlier paper (1903, p. 47) he promises to demonstrate in his final paper that the supposed interference does not exist, but is to be explained by the division of the current, in the way above set forth. In the final paper this promised demonstration takes the following form: "For demonstration of this condition it is not necessary to search out any methods of registration; for this purpose the very objects on which we are experimenting can serve most excellently; a more sensitive galvanometer than *Paramecium*, indeed, one need not demand. Its reactions to the current present unchanging, definite phenomena, taking place in accordance with law, dependent on the strength of the acting current. The orientation with relation to the cathode, the increase in the rapidity of progression up to a definite limit, the changes in the form of the body—all these appear at a definite intensity of the current, which demonstrates in an immediate way that through the bit of detritus and the protist attached to it passes a current of less intensity than in the neighboring fluid, where the reactions of the infusoria are more pronounced" (1903 *a*, p. 55, translation). Now, the question at issue was whether the electric current of a given strength does as a matter of fact always produce the same reaction on the

same organism, as STATKEWITSCH holds, or whether on the contrary the contact reaction may interfere with it, as set forth by PÜTTER and myself. In attempting to demonstrate the former alternative in the manner given above, I submit that STATKEWITSCH merely assumes its truth, and uses this assumption for disproving the second alternative—after which disproof the first alternative of course emerges triumphant. We have here a clear case of reasoning in a circle.

The general fact that the reaction to a certain defined stimulus may be modified by the reaction of the organism to other stimuli, present or past, is perfectly well established for the behavior of lower organisms. In a recent paper (1904, *a*) I have developed this point in detail, and have adduced many examples from the reactions of the Ciliata. The contact reaction is especially effective in modifying the reactions to other stimuli. This appears in the reactions to many agents besides electricity. PÜTTER (1900) has shown that the contact reaction interferes largely with the reaction to heat, a result which I have confirmed, especially for *Stentor*. I have often observed that the contact reaction inhibits to a large degree the reaction to mechanical shock. *Paramecia* and other infusoria when free swimming react strongly to a light touch with a glass point at the anterior end, giving the "avoiding reaction" in a pronounced form. But when thigmotactic they often do not respond at all to such a touch. Again, attached specimens of *Stentor cæruleus* do not react to light in any way, while unattached individuals react decidedly (JENNINGS, 1904). STATKEWITSCH surely cannot expect us to take seriously in opposition to such well defined facts his objection that the concept of the contact reaction is indefinite, and that we cannot *measure* its effect (1903 *a*, p. 56). The effect of the contact reaction on the cilia has been described in a perfectly definite way by PÜTTER (1900) and by myself (1897), and we certainly cannot be asked to shut our eyes to the existence of such striking phenomena because no one has devised means of measuring them.

Irregularities in the Reaction to the Electric Current.—There are certain irregularities in the reaction to the electric

current that deserve mention. First, one often observes that while most of the specimens in a preparation are reacting precisely and strongly, a few specimens do not react at all, swimming about at random. Second, one at times observes single specimens that swim toward the anode, while all the others go toward the cathode. This is most likely to be observed after the current has been reversed several times, though it is sometimes seen at the beginning of the experiment. After repeated reversal of the current, one sometimes makes the following observation. A specimen is oriented and swimming toward the cathode; on reversal of the current it retains its orientation and continues to swim forward—now of course toward the anode. A third very peculiar irregularity that is less unusual than the others is the following. In a rather strong current the animals are swimming slowly and in a rather cramped way toward the cathode. Now the current is reversed, whereupon, without turning around, they swim rapidly *backward* to the cathode. By repeatedly reversing the current, the animals may sometimes be caused to alternate several times, first swimming forward, then backward, retaining throughout the same position. But usually after swimming backward a short time toward the cathode, the animal turns around and swims to the cathode in the usual way. All these irregularities are so comparatively unusual that I have not been able to determine precisely the nature of the ciliary movements.

Reaction of Paramecia to Electricity when in Solutions of Chemicals.—GREELEY (1903) has recently raised anew the question as to the significance of certain peculiarities of the reaction to the electric current when the animals are in solutions of certain chemicals. He points out that in acid solutions *Paramecia* move to the anode, whereas, under usual conditions, where the solution is alkaline or neutral, they move to the cathode. This he attempts to bring into relation with the observations of LILLIE (1903), who shows that cell constituents containing much nucleic acid migrate to the anode as an effect of electrical convection, and that the tendency to migrate to the anode decreases with the decrease in acidity. In this way we seem to be on.

the road to a direct physical explanation of electrotaxis. In criticism of the views of GREELEY, so far as hitherto brought out, the following must be said :

1. All thorough work thus far shows that the essential point in the reaction to the electric current is the method in which the current affects the cilia. No attempt has been made to show how the known effects on the cilia could be produced through the factors emphasized by GREELEY, and it would undoubtedly be difficult or impossible to bring the two into relation.

2. The movement toward the anode is not limited to acid solutions, but is known to take place in a still more striking way in various salt solutions, especially in a solution of sodium chloride. I have observed it even in a solution of sodium bicarbonate, having of course an alkaline reaction.

3. The movement to the anode in such solutions is backward. It has been so described by LOEB and BUDGETT (1897, p. 532), by PÜTTER (1900, p. 297), and so far as I am aware, by every one who has described it carefully, and I can myself confirm this fact. The organisms thus become oriented in the same manner, with anterior end to the cathode, as under usual conditions. Further, these same solutions produce backward swimming even without the use of the electric current. We have then all the existing features of the reaction fully accounted for without taking into consideration the factor considered essential by GREELEY. The electric current taken by itself accounts for the orientation in the usual way; the chemical stimulation taken by itself accounts for the swimming backward; the combination of the two accounts for the swimming backward to the anode.

4. The swimming to the anode continues only as long as the chemical stimulation exists. As soon as the organism has had time to become acclimatized to the chemical, *it swims as usual to the cathode*. This has been shown by PÜTTER (1900), and by STATKEWITSCH (1903 *a*), and I can confirm it. Often it is but a few moments that the swimming backward to the anode continues.

In view of all these facts, it cannot be held on the evi-

dence thus far brought forth, that the phenomena observed in acid solutions, as described by GREELEY (1903), have any special significance for the theory of electrotaxis, such as that author assumes. The known facts point to the following general statement of the phenomena. Immersion in chemicals, of various characters, causes the organism to swim backward. If at this time the *Paramecia* are subjected to the electric current, they continue to swim backward, and, becoming oriented, therefore pass to the anode. This movement to the anode ceases as soon as the stimulating action of the chemical ceases.

In order to make out a case for the theory advanced by GREELEY, it will be necessary to show clearly that this general statement is incorrect.¹

IV. PRESENT POSITION OF INVESTIGATION OF THE BEHAVIOR OF PARAMECIUM.

I believe it may be said that we are now able to make a general, qualitative survey of the chief facts and factors in the behavior of this representative of the unicellular animals. There are doubtless still some dark points; the reaction to the electric current, for example, is still hard to place in the general scheme of behavior, though recent researches have gone far toward clearing up this matter. But it is true that we know, in a general way, most of the chief methods of action of this animal, and the way in which these are affected by the chief classes of external conditions. There still remains the investigation of the intimate physiological processes underlying the gross features of the reactions, and especially the quantitative study of the phenomena which the qualitative examination has brought out. Our present knowledge, then, amounts to a preliminary survey, showing us in the gross the phenomena which require investigation in detail. Attempted quantitative study of phenomena of which the qualitative, purely descriptive, features

¹ Since the above was written, GREELEY'S final paper has appeared (*Biol. Bull.*, Vol. 7, pp. 3-32). It raises many interesting questions, which I hope to touch upon later. (Note added during correction of proof.)

are uncertain, is likely to be misleading and worthless; this has been too often illustrated in the investigations on the reactions of unicellular animals. We cannot measure things till we at least know what we are measuring; if we attempt it our results have only the appearance of accuracy, and are likely to fall to the ground as soon as the qualitative nature of the phenomena is worked out and found to be different from what we had assumed. It is for this reason that the present writer has limited himself thus far almost entirely to qualitative work. Now that the qualitative survey has been made, I believe that if its results are held clearly in mind, quantitative work can be done with some hope of understanding the significance of the data which our measurements bring out. But in view of the peculiar and complicated action system of *Paramecium*, quantitative results will always have to be interpreted with the greatest care, and it must be realized that that method of investigation which examines only the beginning and end of an experiment, without troubling itself as to what the organism does in the meantime, is likely to be most misleading. Further, in view of the peculiar character of the action system of *Paramecium*, and the large part it plays in determining the behavior under stimulation, the utmost caution is necessary in transferring the conclusions obtained with this animal to other organisms having a different action system.

The work on which the present paper is based was done at the Naples Zoological Station while the author was a Research Assistant of the Carnegie Institution of Washington. It is a pleasure to acknowledge my indebtedness to the Carnegie Institution for making the work possible, and for permission to publish the present paper.

Pozzuoli, Italy. April 26, 1904.

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EDITORIAL.

PHYSIOLOGY AND PSYCHOLOGY.

The recognition in daily life as well as in scientific description of two classes of reaction, the psychic and the non-psychic, is the basis of the separation of the science of organic functions into physiology and psychology. Without any assumptions as to the relations of consciousness to organic processes we may, and in fact constantly do, deal with the reactions of organisms according to certain characters which are commonly spoken of as indicative of automatism or intelligence. It is true that we can no more draw a sharp line between the psychic and the non-psychic in reaction than we can between the reflex and the instinctive. Certain aspects or relationships of reactions are so prominent as to furnish the basis of types. Modifiability in high degree is said to be a mark of the psychic, yet no one would deny that the non-psychic reaction is also modifiable. There is surely a difference of degree, but by whom and how is the point at which this characteristic passes from an indication of one type to that of the other to be fixed?

Some physiologists and psychologists have chosen ability to learn as the criterion of the psychic reaction, but this if used alone is evidently of limited and uncertain value, for all reactions, it is safe to assume, change with repetition; organisms profit by experience more or less rapidly. Thus far the critical point which those who have implicit faith in the applicability of this criterion necessarily posit—the point at which ability to learn appears as a distinctive character of the organism, or in the light of the criterion, the point at which the psychic reaction appears in the animal series—has not been discovered. The important question is, Does such a critical point exist?

Few will venture to deny probability to the assumption that modifiability of reaction varies in degree, not in kind; yet, if ability to profit by experience is to be a satisfactory criterion of the psychic there must be either reference to a difference in kind of modifiability, or the choice, by those who attempt to use the criterion, of an arbitrarily selected degree or rapidity of change in reaction as indicative of the transition from the non-psychic to the psychic.

At this point there are at least two possibilities: either we may choose a certain standard of modifiableness as indicative of the psychic reaction, or we may seek for other characteristics in addition to modifiability as means of distinguishing the psychic from the non-psychic in organic reaction. That the latter alternative is the more desirable of the two all who have attempted to use the criterion of ability to profit by experience will grant more or less freely, according to their various prejudices.

Although the physiologist deals primarily with the non-psychic, he is no more able to ignore the psychic than is the chemist to avoid the use of physical concepts and terms. Similarly the psychologist is dependent upon the physiologist, and in turn upon the chemist and physicist, as is the physiologist himself. Granting validity and scientific value to the separation of reactions into the psychic and non-psychic, the existence of physiology and psychology as coördinate sciences needs no justification. Both are natural sciences; both deal with organic reactions. From certain points of view the psychic reaction is more difficult of description than the non-psychic, but the same methods of investigation apply to the two classes of reaction. Physiologists and psychologists must coöperate in discovering, and must agree upon the distinguishing characteristics of the psychic and the non-psychic reaction. By mutual agreement they must fix the limits of their sciences.

The most keenly felt need at present in the science of organic reaction is for careful, detailed, patient, and extensive study of the forms and modifications of reaction. Whether physiologists or psychologists, we must know our materials

thoroughly before we can classify them or profitably consider their relations to the materials of allied sciences; in fact even before we can distinguish physiology from psychology in any accurate sense we must know the possible methods of classification of reaction, and be able, in the light of accurate and extensive knowledge of the peculiarities and unimportant variations of reactions as well as their fundamentally important differences, to select as criteria those characters which are most constant and which taken together form the most valuable working basis for the sciences of reaction.

There is a tendency among physiologists—among natural scientists generally—to look upon psychology with distrust, if not with indifference or scorn. The average German physiologist uses very different tones of voice for the “*Physiolog*” and the “*Psycholog*.” Some of them apparently feel that psychology is too near akin to metaphysics to be a safe favorite for the natural scientist, while others are evidently satisfied in their own minds that the psychic is not and cannot be material of a natural science. In America too there is a strong prejudice against psychology, among the natural scientists especially, or, if not prejudice, there is a distrustful curiosity which makes the life of the truly scientific student of psychic reactions at times unpleasant. This general distrust and ridicule of psychology is doubtless due, first, to the fact that the naturalistic movement of the last century was accompanied by a wide spreading and deep distrust of the speculative sciences of which psychology was then, and is still by many, reckoned as one; and second, perhaps almost as largely, to the semi-scientific and too often carelessly used methods of that new psychology which called itself experimental. Even the honest and sincere defender of psychology, or of the possibilities of such a science, cannot deny that much work which has been placed upon record as experimental psychology is pure rot. But, admitting this with regret, he well may ask, What of the early stages in the development of astronomy, of chemistry, of physics, of anthropology, of sociology? Natural sciences are not born to perfection of method, they develop; and psychology is even now approach-

ing a stage of development which will justify its recognition by the most timid, narrow, or prejudiced naturalist as an increasingly exact natural science. Sciences differ widely in degree of exactitude; at present, for example, the biological sciences are far less exact than the physical, but one may reasonably argue that this is due to inherent difficulties in dealing with the materials rather than to the impossibility of applying exact methods. Psychology as a natural science, or rather psychology in so far as it is considered as a natural science, is in its infancy. As physiology gradually approaches the standard which physics has set for it, so psychology approaches, and will the more rapidly approach as those in allied fields recognize its progress, this same standard.

For those of us who have at heart the establishment and advancement of comparative psychology as a science coördinate with physiology there is the clear duty to make our work eminently worthy of scientific recognition and reliance. Casting philosophical implications aside, so far as our scientific work is in question, we should apply ourselves to the study of psychic reactions with intent to place our knowledge of them on a level with or above that of the non-psychic as represented by the condition of present day physiology. In attempting to do this we should ever be willing and eager to take advantage of the assistance which the closely allied biological and less directly related physical sciences can give us. Speculative sciences have their place, but we shall accomplish most for the science of psychic reactions if we keep our metaphysical longings in the background and strive ceaselessly for accurate and complete descriptions of the reactions with which we are concerned—reactions which are the most complex and interesting of biological phenomena.

ROBERT M. YERKES.

CLARENCE LUTHER HERRICK.

We are called upon with the present issue of the *Journal* to lament the sad and untimely death of its founder and editor-in-chief at Socorro, New Mexico, on the 15th of September. For the past ten years, dating from his last connection with Denison University, he has struggled heroically against tuberculosis of the lungs, together with other complications, which at last cut him off in the midst of his labors and in the prime of life. Untimely as his death must seem when regarded from the point of view of his plans and hopes, yet Dr. HERRICK had done an amount of scientific research and philosophical writing, some of which he was preparing for the press when he was taken, which assures him an enduring name in the world of thought.

The end came in accordance with his own most earnest wish—he fell fighting for the truth. As one of those who were near him when he passed away has said: “He was taken literally in the harness. His laboratory and study tables showed the unfinished tasks. His morning mail brought its usual load of duties. He had contributed an article to the September number of the *American Geologist*, and his mail on the morning of his death, brought a request from Dr. N. H. WINCHELL for some further contributions to the October number. Thus in the midst of his labors he passed into the larger sphere.”

Very early in his career he seems to have laid out, at least in a general way, a plan of action, including for the first part of his life miscellaneous research and study under direction in the broad field of general natural history. Upon the basis of this foundation, was to follow a period of intense specialization in a circumscribed field of zoological work leading up to a mastery

of the anatomy and physiology of the nervous system. Finally the ripest years were to be devoted to physiological and comparative psychology on the basis of the mechanics of the nervous system and to philosophical correlation.

His life may be roughly divided into four periods. While these were marked by extraneous events and were apparently purely artificial and arbitrary, yet it may be said that the ideal scheme was in the end fairly achieved, though with great deviation in the details of the working.

Dr. HERRICK was born near Minneapolis, June 21, 1858. He grew up in a home far from neighbors, a solitary child with few playmates, and very early showed his bent as a naturalist. While still in the Minneapolis High School he collected extensively and left at graduation a case of over a hundred mounted bird skins and other specimens to the high school. It was during this period that his father, despite his poverty, got him an eight dollar microscope. With this crude instrument and without guidance or library facilities he worked over the fresh water fauna of the neighboring brooks and pools so thoroughly that before graduation from the University of Minnesota in 1880 he had published several articles of value on the fresh water crustacea of Minnesota and four years after graduation, with somewhat better facilities, published a report on the micro-crustacea of Minnesota, which is still standard. The materials for this report were elaborated before he graduated from college.

These years were filled with many bitter struggles, not the least of which was with poverty and the consequent lack of material for study. But, notwithstanding, he completed the college course in three years, at the same time partly supporting himself by assisting on the staff of the Geological and Natural History Survey of Minnesota. He had also showed so obvious a native gift with his pencil that upon his graduation the president of the university said to his father that he was uncertain whether to advise the young man to devote his life to science or to art. But there was no uncertainty in the mind of the graduate. Continuing his work on the Geological and

Natural History Survey of Minnesota, he published many papers in rapid succession on the fauna of the state and began an extensive report, the first volume of which was completed in 1885. This was a large quarto on the Mammals of Minnesota, fully illustrated with many colored plates and pen drawings. It was accepted for publication, but for lack of funds in the Survey never saw the light. Years afterwards, in 1892, a small octavo was published by the Survey made up of the more popular parts of this work. The remainder is still buried in the vaults of the Survey in Minneapolis. The season of 1881-2 was spent at the University of Leipzig, and in 1883 he was married to Miss Alice Keith of Minneapolis. This, roughly, may be said to constitute the first period of his life, from 1858 to 1884.

He was called to the chair of Geology and Natural History of Denison University in the summer of 1884. He spent the fall of that year at Denison, then returned to Minneapolis to complete the work in progress in the Minnesota Survey, and in the fall of 1885 moved with his family to Granville. Meanwhile, in 1885, he took the degree of M.S. from his *alma mater*. It had been his intention to continue his zoological work, and there was great activity in this line during the entire period, but the routine excursions made in the course of the instruction of his geology classes showed him so much of interest in the local strata that his chief labors while in Granville were upon the fossils and stratigraphy of the Waverly free stones and shales of Ohio. This work was abruptly cut short by his removal from Granville in 1889 and, while never rounded out as he would have liked, is probably his most important geological work. In 1885 he founded the Bulletin of the Scientific Laboratories of Denison University, in which the greater part of his researches, and those of his pupils, on Ohio geology were published.

His phenomenal success as a teacher during this and the subsequent periods was due to factors, some of which are easily seen—others are harder to define. After his attractive personal qualities and magnetic enthusiasm, I should place his deep philo-

sophic insight and the fearless way in which he disclosed his profoundest thinking to the least initiated of his pupils. The ability to do this without befogging the air was an exceedingly rare gift and was stimulating even to a dullard. He knew the philosophical classics thoroughly from original sources and the trend of his thinking was very early foreshadowed in the translation of LOTZE's *Outlines of Psychology* published in 1885 in Minneapolis, with his own appended chapter on the structure of the nervous system.

Upon his removal to the University of Cincinnati in 1889, with which the third period of his life may be said to begin, the geological studies with which the preceding five years had been so fully occupied were summarily brought to a close and he threw himself with renewed energy into the study of the nervous system. Extensive papers on the brains of different animals appeared in rapid succession, of which the most valuable are two series, one on the brains of various fishes, the other on those of reptiles. In 1891 the *Journal of Comparative Neurology* was founded and served as the medium of publication for most of these researches. The founding of this Journal can best be designated as a piece of characteristic audacity. It was a purely private enterprise, with no fund to defray the expenses and very little outside coöperation promised. But without counting the cost he plunged boldly in, expecting a constituency to be developed as the work went on. In this he has not been disappointed, though recognition of financial needs has lagged sadly behind that of the scientific value of the Journal.

At the close of 1891 he resigned his chair in the University of Cincinnati to accept a chair of biology in the University of Chicago, then being reorganized. The early part of 1892 was spent in Europe, chiefly Berlin. Upon his return the adjustment at the University of Chicago presented unexpected difficulties and after a series of misunderstandings he finally withdrew from that institution, declining an offer to return to Germany for further study on full salary. He was immediately elected to his old post in Denison University with an assistant and the privilege of devoting only a part of his

time to teaching, the remainder, either at home or abroad, to the further prosecution of his research. A year and a half of great productiveness followed. He bought a small tract of land adjacent to the college campus, built a residence upon it and planned to devote the remainder of his days to breeding animals on an extensive scale and studying the laws of heredity, comparative psychology and allied problems. But before this project was fully under way his health broke down completely and he was forced to abandon his home in the fight for life.

In December, 1893, he had a severe attack of la grippe, but, as was his custom in illness, went on with his work as usual. Upon completion of the last examination of the term he came home too ill to correct the papers, and in course of the following night was attacked by a severe hemorrhage from the lungs and for weeks his life hung in the balance. With the return of spring his strength increased sufficiently to enable him to remove to New Mexico, where the local physicians told him that he had a fighting chance for a few years. He accepted the challenge bravely and for more than ten years held the disease in check. During the spring of 1894 his college dedicated the Barney Science Hall, which had been built largely under the stimulus of his presence in the faculty; but he was never permitted to work in it.

The fourth period, from 1894 to 1904, covers the remaining years of his life.

This decade, filled with bodily pain and the worse torture of anxiety and mental unrest, is yet one of the most productive periods of his life. Much of the time was spent in the open with covered wagon and camp kit, and with the return of strength scientific interests again absorbed his attention. Naturally in this case he again turned to geology and an extensive series of articles on the geology of New Mexico bears testimony to the industry of these apparently aimless wanderings. The first scientific work done in the Territory, however, was a revision of his earliest important work, the Crustacea of Minnesota. As soon as his geological knowledge became known his services were in demand as a mining expert and during the later

years of his life in the Territory he supported himself and his family chiefly by practicing this profession as strength permitted. In 1898 he took the degree of Ph.D. from the University of Minnesota. For four years (1897-1901) he was president of the territorial university at Albuquerque, though at the close of the third year it became evident that the strain of the executive work and confinement were too hard for him, and the connection during the fourth year was mainly one of supervision and general control.

During his last year there was an obvious failing of physical strength, so that long field trips had to be abandoned. But the more quiet life gave opportunity for a thorough recasting of many questions and formulation of matters which had been in his mind all his life. So that before his death much of the philosophical correlation, of which mention has been made, was effected. A number of articles have already been published in the philosophical serials bearing on these matters and there is a considerable collection of MSS. remaining, much of which can doubtless be edited for publication. It is gratifying to know that he had the satisfaction of seeing this work so well rounded out before his death and that the latest months of his life were much more restful than those preceding, some of which were marked by extreme suffering. He continued in about the usual health until September 8, when he again had a series of uncontrollable hemorrhages, daily becoming weaker until on the morning of the 15th he peacefully passed away.

One essential feature of his success must receive mention here—the devoted heroism of his wife. His work was always stimulated by her interest and coöperation; but during the last decade his life was unquestionably preserved by her self-sacrificing care. She often accompanied him for weeks on wagon trips far from settlements in order to see that he had proper food and comforts, sometimes enduring severe hardships and sacrificing her own health for his welfare.

So much for a brief sketch of Professor HERRICK's life. Of his relation to the various institutions with which he was

connected and the great stimulus which he gave to education by his connection with them, an account will be given in other biographical notices soon to appear in the Bulletin of the Scientific Laboratories of Denison University, which he founded. It remains here to say something of Dr. HERRICK, first, as an investigator and thinker, and secondly, as a teacher and as a man.

In estimating the character of his work it is difficult to say whether he was primarily an investigator or a philosopher. And this is to his great credit for he combined in a remarkable degree the qualifications of an expert in both of these lines. He had at once acute perceptions, and keen insight for scientific details, and a broad philosophic horizon and perspective which peculiarly fitted him for the work he undertook of throwing light upon the nature of consciousness from the neurological side. A glance at the appended bibliography will show that a philosophic scope as well as a scientific specialization characterized all his work.

His work in every line was extremely suggestive, and it should be added, seldom exhaustive, though certain of his neurological and geological papers reveal his power of accurate and detailed research. But his thought ever was moving forward, and he was impatient of the routine details which would put any check upon his richly developing insight.

His scientific labors fall in three states—Minnesota, Ohio, and New Mexico. Of his work in geology during the first and second periods of his life we have already spoken. His neurological work was done mostly during the second and third periods, while connected with the University of Cincinnati and with Denison University.

The first contribution in neurology was the elementary chapter on the nervous system appended to the translation of LORZE's *Outlines of Psychology*, published in Minneapolis, in 1885. This is significant not so much for its content (though here the dynamic point of view is dominant) as for its context. The juxtaposition, in a manual designed for an elementary text-

book, of LOTZE's lectures and original lectures on the mechanism of the brain was a decided novelty in those days.

In 1889 he began work in earnest on the nervous system and immediately there appeared a series of papers in rapid succession, some of great length and others mere jottings. The first long paper was published with Professor W. G. TIGHT in the Denison University Bulletin in 1890, and was entitled "The Central Nervous System of Rodents." This paper contains nineteen double plates and a vast amount of observation; and was designed as a preliminary survey of the field, the plates to form the basis of further detailed observations and correlation. But he soon became convinced that this correlation could best be attempted after a thorough study of several types of lower brains and the series was interrupted. At the time of his breakdown in 1894 he was just about to take up again by the degeneration methods a more thorough study of the mammalian brain. Thus this rodent paper stands now as an unfinished fragment.

This, however, illustrates well his plan of work, a plan which must be clearly understood in order to put a proper estimate on his published researches. He found correlation impossible and at once saw that only in primitive types could the key be found, and that too not in any one series, but only in the common features of many lower types. Accordingly he undertook to examine in rapid succession as material offered a large number of lower brains, taking voluminous notes and publishing the *observed* data as fast as they were ready. All of this work was fragmentary and much of it contained but little correlation. But the mass of facts gathered and recorded was enormous. He realized that the incessant strain on his eyes could not always be kept up, and planned to accumulate fact as rapidly as possible, until failing eyes should impair his efficiency in this field. *Then* he hoped to review the whole field of vertebrate neurology systematically, using his own observations as the skeleton on which to build by study of literature and further research of his own on critical points, until the whole should take shape as a unity. When he settled in Granville

the second time in 1893 he expected to begin that work of correlation, and this is doubtless the special significance of the announcement published at that time of a text-book on comparative neurology. But this period of work he was not able to enter far and the text-book is still unpublished. This manuscript, together with that of several other projected works on psychology and ethics, remains. It is yet too early to state how much of this matter can be edited for publication. If the last ten years of his life could have been spent in Granville, as was his plan, results of moment in the way of correlation would undoubtedly have followed. As it is, none of the papers in neurological lines were regarded by him as other than fragments.

The first important paper in neurology was published in the *Journal of the Cincinnati Society of Natural History*—"Notes upon the Brain of the Alligator." This is an elaborate descriptive article illustrated with nearly a hundred of the beautiful pen drawings which he used so freely in all of his work.

The second neurological paper of special importance was the leading article in the first issue of this *Journal*, on the histogenesis of the cerebellum in correlation with its comparative anatomy. This paper was ignored largely by the workers immediately following, but its main points have been fully confirmed by later students. It is really, though very brief, one of his best contributions.

Of the remaining neurological papers, the most important were published in this *Journal*, those in the *Anatomischer Anzeiger*, *American Naturalist*, etc., being for the most part summaries of the longer articles. These were descriptive articles, in most cases, devoted mainly to the brains of fishes and reptiles, with some attention to amphibians.

The greater part of his descriptions of the fish brain have since been worked over with the same sections which he used in hand, and his descriptions have been found to be very exact, though often so brief as to make it difficult to understand them without reference to the preparations. Furthermore they stand the test of control by the more recent neurological methods very well, though of course not always in detail. His method

of pushing a given research through rapidly enabled him to cover a great deal of ground with surprising fidelity to the facts of his material. But the method results in a positive hardship to his readers, since the matter was not fully digested and correlated before publication. While, therefore, this matter is of great value, it is hard to read and will not be used fully save by a few specialists until it is worked over and correlated within itself and with other more recent work. It is hoped that this may be done soon. The facts as stated must necessarily serve as the basis for any future work on the types which he studied.

After his departure for New Mexico a few brief neurological articles were published, but only fragments remaining from his earlier work or critical articles. This period was devoted chiefly to geology and other studies which could be pursued out-of-doors, and more recently to philosophical writing.

In 1892 he contributed a short paper to the LEUCKART Festschrift. In 1893 he wrote four articles for the supplement to Wood's Reference Handbook of the Medical Sciences. He also wrote a few articles for the second edition of the Handbook, beginning in 1900. In conjunction with C. JUDSON HERRICK, he prepared the neurological articles for the BALDWIN Dictionary of Philosophy and Psychology, some of these being encyclopedic articles of considerable length.

The best years of his life were devoted to his neurological work and it is all of a high order of merit, yet one feels that in very little of it did he do himself justice. His impetuous temperament and phenomenal ability to turn off research rapidly is partly responsible for this; but its unsatisfactory character is largely due to the fact that it was cut off prematurely. He never had the patience to polish his work as some like to see it done, and it would have been much more accessible if he had put even the unfinished reports of progress into more systematic form. Yet, even as it is, the aggregate is a monumental work to stand as the out-put of only about half a decade of productive work.

Of his work in New Mexico one who had first-hand knowledge writes as follows:

“He first resided, with his family, in Albuquerque, and while gaining strength, began to study the local fauna and flora. Perhaps it may be allowable to give an incident from this period of his life, for it is most typical of him.

“While recovering strength he was accustomed to lie upon a couch in the open air. His microscope was close at hand, and he began at once the study of our fresh water crustaceans. For a few minutes he would study his creature under the microscope, make his exquisite drawings, write out his description, when, being seized with a coughing spell, he would be forced to his couch completely exhausted, to remain there perhaps half an hour before he could resume his study.

“This incident illustrates two characteristics. It illustrates first, his unremitting labors. Only when necessity compelled did he cease his labor. True, he had his recreations, but these were often of such a character as to be downright labor for most men. The incident also illustrates, secondly, his deep thirst for knowledge. Only he who has drunk at the fountain of inspiration could labor so incessantly under conditions so unfavorable.

“After some months spent in Albuquerque, Professor Herrick and his family moved to Socorro. There he became interested in geological studies, and also collected a considerable herbarium of native plants. He contributed occasional articles to the *Journal of Comparative Neurology*. In the spring of 1897 he, in company with his son Harry and Dr. MALBY, made an exploring trip to the Tres Marias Islands, off the western coast of Mexico, where a large natural history collection was made.

“Upon his return from Mexico, Professor HERRICK was elected President of the University of New Mexico, and began his new labors in 1897. His wide experience, having been connected with three universities, viz., Minnesota, Cincinnati and Denison, his several trips to Germany, where he met and worked with the leaders in the biological sciences, his national reputation in fields of zoology, geology, neurology, psychology and philosophy, gave him an ideal preparation as a college president. No wonder, then, that he drew to him immediately a

number of advanced students who were inspired by his genius and broad knowledge, and who fairly worshiped him.

"In passing, it may be mentioned that under him the policy of the University was completely reversed. From a literary academy, it became a scientific school; from a preparatory school it developed into a college with a post-graduate department. In three short years the institution was placed where it belonged—at the head of the school system of New Mexico.

"Upon entering his new duties, Dr. HERRICK commenced the biological and geological survey of the territory.

"Two volumes of original investigations in these lines speak for themselves. In addition, contributions were made to some of the leading journals of America, especially to the *Journal of Comparative Neurology*, the *American Geologist* and the *Psychological Review*."

Of Professor HERRICK's contributions to philosophy a word should be said. That his interest was a deep and abiding one is abundantly evident from a glance at his writings which include many articles and discussions dating from the publication in 1882 of his translation of LOTZE's lectures on psychology to the series of articles on "Dynamic Realism" which he had begun to publish in the *Journal of Philosophy, Psychology, and Scientific Methods*, at the time of his death. He made frequent short contributions to the *Psychological Review*, besides publishing various articles of a psychological and philosophical character in the columns of his own *Journal*. His interest in problems of ethics and religion is evidenced by divers articles in certain of the religious periodicals as well as by much unpublished MS.

Of his metaphysical writings it should be said that they were always inspired by his scientific researches. He never was satisfied with the easy philosophy of the "anti-metaphysical" standpoint of many fellow scientists. Psycho-physical parallelism he regarded as "the Great Bad." The aim of his life was to throw light upon just such so-called insoluble problems as the relation of consciousness to the brain. "Ignorabimus" is a word which never fell from his lips. The unity of

the material and the mental is a truth upon which he came to lay increasing stress in his later years. Starting from a Lotzean spiritualistic idealism he never lost hold of the monism which characterizes that philosophic world-view, though in many respects he worked beyond it, his scientific studies serving to correct any tendency to an exclusive emphasis upon the mental. This is seen in the title under which his latest writings appear—"Dynamic realism"—in which many will find hints of a coming philosophic movement which is to reinterpret the fixed ontological categories of a past metaphysics in more dynamic and organic terms.

Of his contributions to the theory as to the nature of consciousness (equilibrium theory or consciousness), the physiological basis of the emotions, theory of pleasure-pain (summation-irradiation theory of pleasure-pain), his discussion of the reflex arc or organic circuit under the terms of his own coining ("aesthesodic" and "kinesodic"), and in general his interpretation of experience in dynamic and energetic terms, we may not here speak in detail. But the attention of the readers of this *Journal* should be called to this side of his work as it is embodied in his various published writings and especially in certain writings which are yet to appear.

In the memory of his pupils Professor HERRICK was greatest as a teacher. This statement can only be appreciated by those who knew him personally and were in his classes. There was no display or oratory. He was not what would be called a gifted public speaker, though he was often called upon for such services. It was in the class-room or about the seminar table or in general conversation that the inexhaustible fertility of his thought and fine suggestiveness of his language appeared. In his lectures one always knew that he was getting the best, the latest, the deepest results of his scientific research and philosophic reflection. Never was any work slighted in which his students were involved. Other things might be sacrificed—time, money, convenience, even health itself, but never the student. The result was that his teaching was not confined to the class-room or laboratory. There never was an occasion

upon which he was not ready to suggest, advise, assist the groping mind in its search for the truth.

He was extraordinarily versatile in the class-room. He would lecture with a piece of chalk in each hand, sketching at the same time ambidextrously upon the blackboard the figure he was describing. Never did the lecture degenerate into a mere description of the figure. The figure he was describing was the figure in his mind, the figure that he was thereby suggesting in the student's mind. Such description and all the other instrumentalities of the class-room and laboratory were always kept in their proper place and proportion as means to the end of knowledge and insight. His artistic sense was too fine to allow them ever to degenerate into mere ends in themselves; the technique of his teaching was in itself a work of art, the more that it was unconscious on his part. His courses in neurology, embryology, and histology were primarily courses in thinking. This is no doubt the reason why so many of his students look back upon his teaching as the period of their intellectual awakening.

One of his colleagues at Denison University says of him: "All who knew Professor HERRICK loved him. Different friends had different reasons for loving him, but all agreed in loving. Christian people loved him because he was a loyal Christian man. Intellectual people loved and admired him because of his brilliant and keen intellect; and men in general loved him because they saw in him a true and noble man loving the truth and living it out in his daily life."

As has been said of another: "He did his work with a quietness which concealed its power. He contributed to science our best example of the scientific temper. He was a profound thinker. He was a successful teacher. He was a lover, inspirer, and leader of youth."

H. HEATH BAWDEN.

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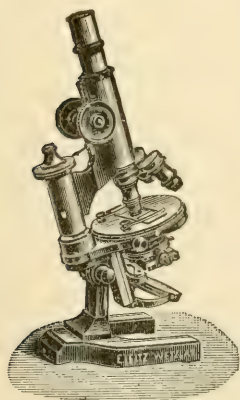
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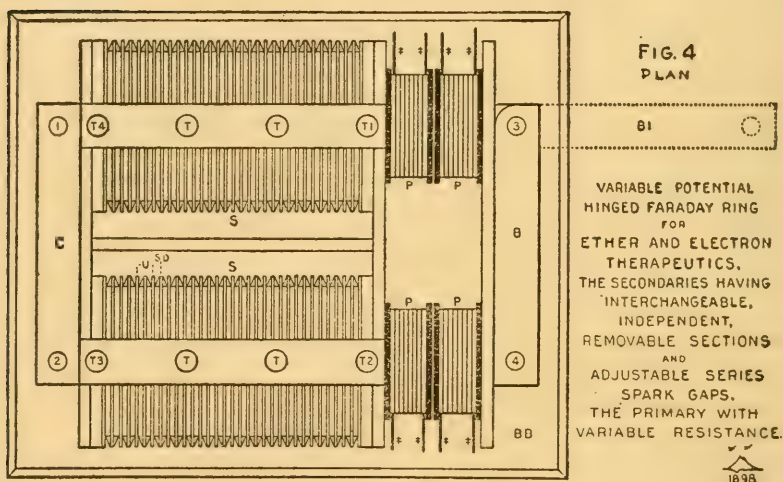
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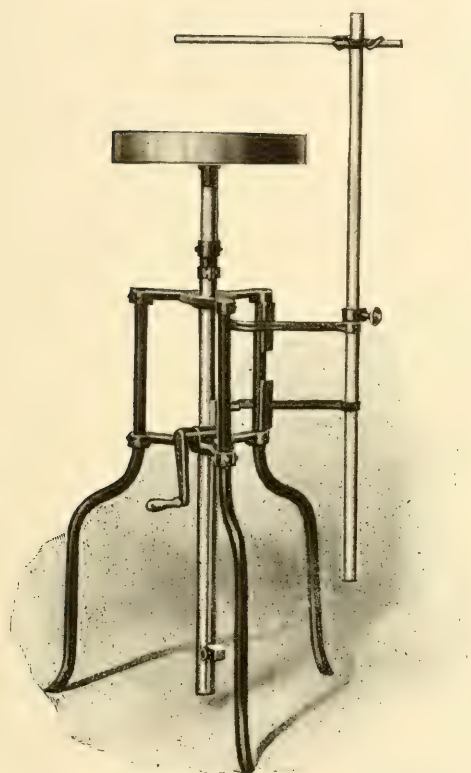
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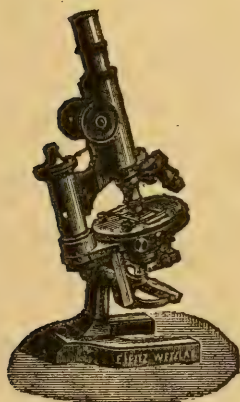
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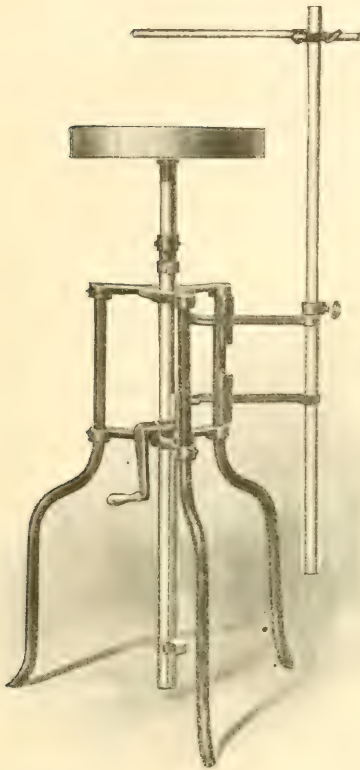
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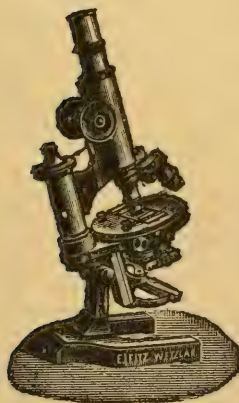
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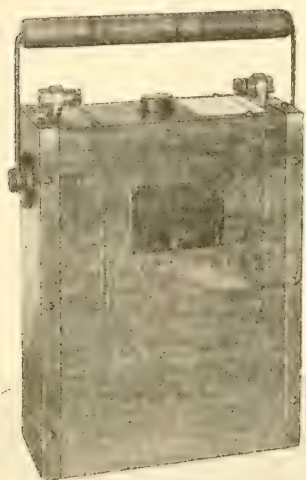
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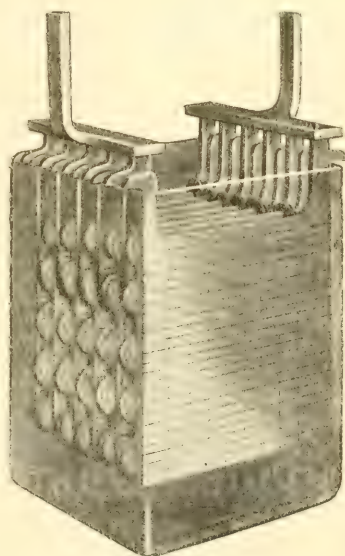


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